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RESPONSE OF TWO CLONAL STRAINS OF TRIUMPH POTATOES TO VARIOUS CONTROLLED ENVIRONMENTS [1]

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INTRODUCTION

In a previous publication the writer reported the response of one strain of Triumph potatoes to gradually changing photoperiod and temperature and to abrupt changes in photoperiod and nitrogen supply.[2] Further experiments have been conducted to determine whether other strains or varieties would respond in a similar manner to different environmental treatments. The environmental conditions under which tests were made involved different levels of nitrogen nutrition, constantly long or short days in contrast to gradually changing day lengths, and long or short days at several temperatures. Because of the difficulty of arriving at a satisfactory evaluation of a strain or variety by field tests [3] another objective was to determine whether varieties or strains can be analyzed as to their adaptation to various latitudes by testing them under controlled conditions with the photoperiods and at temperatures characteristic of certain latitudes.

EXPERIMENTAL METHODS

During the winters of 1934–35 and 1935–36 Triumph potatoes of two or three clonal strains were grown in the greenhouse with nutrient solutions in essentially the same manner as described in an earlier publication.[4] In 1935–36 the nitrogen-deficient treatment was provided by using only 10 percent as much nitrogen in the solution as was used in the complete solution. Six weeks after the plants emerged this was increased to 20 percent. These plants manifested very distinct nitrogen-deficiency symptoms. Photoperiods of specific duration were provided by 100-watt bulbs placed about 3½ feet apart and maintained about 2 to 2½ feet above the tops of the plants (fig. 1). All lights were turned on at 7 a. m. so as to avoid the variable light conditions incident to the beginning of midwinter days. Lights were turned off whenever daylight seemed brighter than the artificial light.

[1] Received for publication November 27, 1939. Paper No. 243 of the Journal Series of the Nebraska Agricultural Experiment Station.

[2] WERNER, H. O. THE EFFECT OF A CONTROLLED NITROGEN SUPPLY WITH DIFFERENT TEMPERATURES AND PHOTOPERIODS UPON THE DEVELOPMENT OF THE POTATO PLANT. Nebr. Agr. Expt. Sta. Res. Bul. 75, 132 pp., illus. 1934.

[3] WERNER, H. O. PERFORMANCE OF CLONAL STRAINS OF TRIUMPH POTATOES. I. TRIUMPH STRAINS ON DRY LAND IN WESTERN NEBRASKA. Amer. Potato Jour. 17: [66]–80. 1940.

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——— PERFORMANCE OF CLONAL STRAINS OF TRIUMPH POTATOES. IV. COMPARISON OF TRIUMPH STRAINS IN EASTERN NEBRASKA (AT LINCOLN) WITH AND WITHOUT IRRIGATION. Amer. Potato Jour. 17: [153]–155. 1940.

——— PERFORMANCE OF CLONAL STRAINS OF TRIUMPH POTATOES. V. COMPARISON OF TRIUMPH STRAINS IN VARIOUS SOUTHERN STATES. Amer. Potato Jour. 17: [174]–181. 1940.

[4] See footnote 2.

In the late afternoon lights were turned on whenever artificial light was brighter than natural daylight. On dark days lights were left on throughout the day. Temperature was thermostatically controlled so that the desired mean was secured during each 24-hour period. The day temperature was 10° to 20° F. higher than the night temperature. With "southern" or "northern" conditions photoperiods and temperatures were changed once each week to simulate changes that occur during the potato-growing seasons in the different

FIGURE 1.—Potato plants growing under "southern" conditions (S34). Photographed January 14, 1935.

latitudes. The general characteristics of the various treatments are outlined in table 1. In 1934–35 the southern-day conditions were similar to those that prevail in southern Louisiana and the northern ones simulated a cool season in northwestern Nebraska (fig. 2).[5] [6] In 1935–36 the southern-day conditions were similar to those of far southern points, such as Brownsville, Tex., or Homestead, Fla., and the northern conditions resembled those of northwestern Nebraska in a warm season (fig. 3). The plants of one light or temperature treatment were necessarily grouped in one part of the greenhouse, but plants harvested on each date of each strain within a treatment were

[5] MARVIN, C. F. SUNSHINE TABLES. 3 v. 1905. Part I, Latitudes 20° to 30° North (reprinted), W. B. 805, 1923; Part III, Latitudes 40° to 50° North, W. B. 320, 1905.

[6] MARVIN, CHARLES F. NORMALS OF DAILY TEMPERATURE FOR THE UNITED STATES. U. S. Weather Bur. Monthly Weather Rev., Sup. 87 pp., illus. 1925.

distributed throughout the area so as to equalize place variations. When two nutrient solutions were used the plants that received the same solution were randomized throughout the greenhouse area.

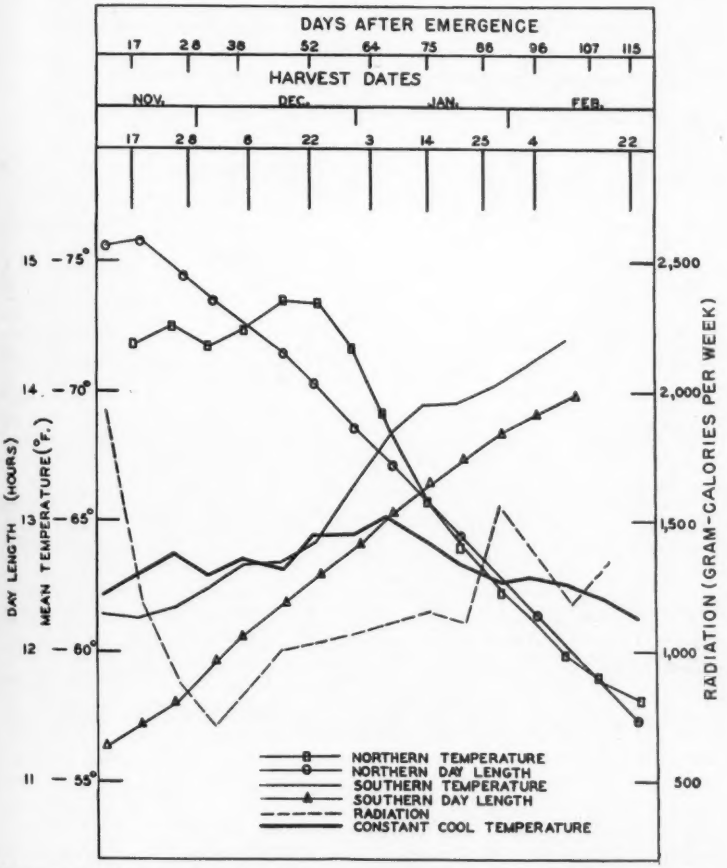

FIGURE 2.—Environmental conditions in the winter of 1934–35, showing mean temperature, day length, and radiation (measured as gram-calories per square centimeter) for weeks ending at points designated on the various graphs, and days after emergence of plants of the northern and southern series, N34 and S34.

Light-intensity readings were secured at the United States Weather Bureau station about one-fourth of a mile from the greenhouse. Light intensity was greater in 1935–36 than in 1934–35. However, there were 2 weeks of dark days in January 1936 and these caused a noticeable slowing down of tuber growth.

In order to simplify matters as much as possible the first part of the discussion (pp. 765–785) of results will deal with the influence of

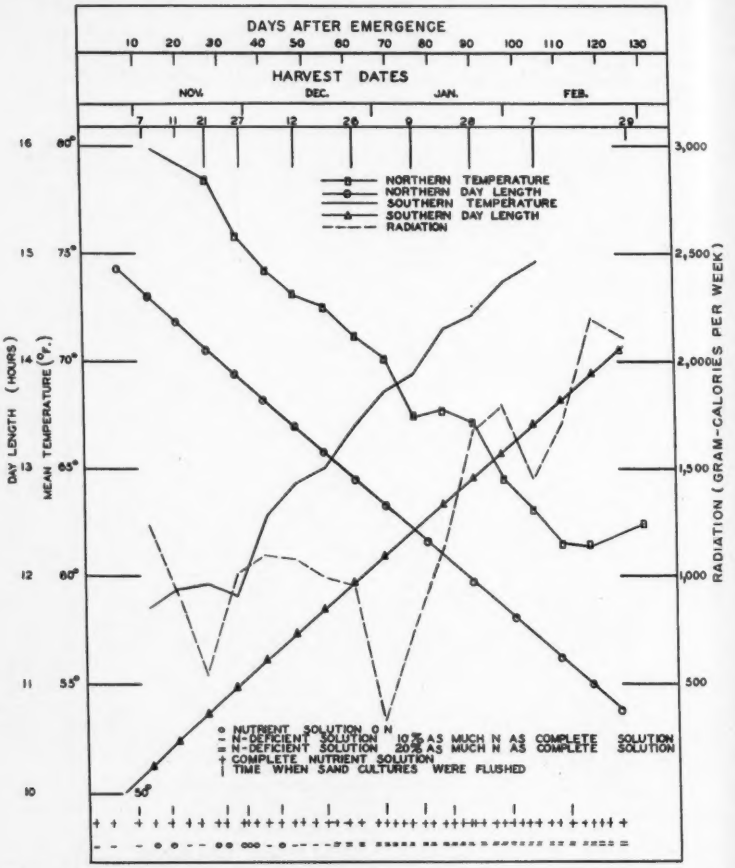
DAYS AFTER EMERGENCE
10 20 30 40 50 60 70 80 90 100 110 120 130
HARVEST DATES
NOV. DEC. JAN. FEB.
7 11 21 27 12 26 9 28 7 29
NORTHERN TEMPERATURE
NORTHERN DAY LENGTH
SOUTHERN TEMPERATURE
SOUTHERN DAY LENGTH
RADIATION
DAY LENGTH (HOURS)
MEAN TEMPERATURE (°F.)
RADIATION (GRAM-CALORIES PER WEEK)
16 80° 3,000
15 75° 2,500
14 70° 2,000
13 65° 1,500
12 60° 1,000
11 55° 500
10 50°
NUTRIENT SOLUTION 0 N
N-DEFICIENT SOLUTION 10% AS MUCH N AS COMPLETE SOLUTION
N-DEFICIENT SOLUTION 20% AS MUCH N AS COMPLETE SOLUTION
COMPLETE NUTRIENT SOLUTION
TIME WHEN SAND CULTURES WERE FLUSHED

FIGURE 3.—Environmental conditions for 1935–36 treatments, showing mean temperature, day length, and radiation (measured as gram-calories per square centimeter) for weeks ending at points designated on the various graphs, and days after emergence of plants of the northern and southern series, N+, and N−, S+, S−. Symbols at bottom indicate date on which nutrient solutions were applied as explained by legends within the figure.

the environment on one strain (the very early strain No. 12) and the latter part (pp. 785–788) will deal with the differences between strains under the different conditions.

TABLE 1.—*Essential characteristics of the various treatments used in growing strains of Triumph potatoes*

Treatment designation		Day length	Range of mean daily temperature during each treatment	Season when plants were in greenhouse	Nitrogen in nutrient solution	Plants of each strain harvested on each date
Symbol	Descriptive name					
		Hours	*° F.*			*Number*
11C	11-hour, cool	11	62 -65	Oct. 20, 1934, to Feb. 22, 1935	Complete	2
16C	16-hour, cool	16	62 -65	do	do	2
S34	Southern	11 -14	61 -72	Nov. 1, 1934, to Feb. 4, 1935	do	3
N34	Northern	14.5-11.6	72. 5-58	Nov. 1, 1934, to Feb. 22, 1935	do	3
S+	Southern, balanced solution.	10 -14.1	58. 5-75	Oct. 25, 1935, to Feb. 29, 1936	do	4
S−	Southern, nitrogen-deficient.	10 -14.1	58. 5-75	do	10–20 percent.[1]	4
N+	Northern, balanced solution.	14.9-10.8	80 -61	do	Complete	4
N−	Northern, nitrogen-deficient.	14.9-10.8	80 -61	do	10–20 percent.[1]	4
S++	Southern ++N [2] (bright sun).	11.7-15	65 -75	Mar. 2, 1935, to June 1, 1935	++	4
S+−	Southern +−N [2]	11.7-15	65 -75	do	+−	4
S−−	Southern −−N [2]	11.7-15	65 -75	do	−−	4
S−+	Southern −+N [2]	11.7-15	65 -75	do	−+	4

[1] 10–20 percent of the nitrogen in the complete nutrient solution (see fig. 3).
[2] ++N=complete nutrient solution the first 4 and remaining weeks; +−N=complete solution first 4 weeks and after that solution with 10 percent as much nitrogen (or −N); −−N=nitrogen-deficient solution both periods; −+N=nitrogen deficient solution only during the first 4 weeks.

RESPONSE OF VARIOUS PLANT PARTS UNDER DIFFERENT ENVIRONMENTAL CONDITIONS

VEGETATIVE GROWTH

Vegetative growth of the plants, as measured principally by dry weight on successive dates, was very much restricted when the days were short and cool in the early part of the season (11-hour cool days (11C)[7]) and under southern conditions (S34, S+, S−; figs. 4, 5, 6). Under these conditions vegetative growth was restricted almost entirely to the main axis, the terminal inflorescence of which aborted while in the primordial stages. During most of the season the leaves were a pale green, becoming glabrous quite early, the outer leaf edges turning downward. The elongation of the main axis was practically accomplished by the seventeenth day. After that the increase in weight resulted from leaf expansion, stem thickening, and stolon production. There was relatively little vegetative growth beyond the thirty-fifth day. After the sixtieth to seventieth days there generally was no increase in vegetative dry weight but frequently a decrease (fig. 5). This decrease was most evident in plants grown with 11-hour cool days (11C), and with those under southern conditions in 1934–35 (S34). It was accompanied by the yellowing and death of lower leaves. These early short-day plants were relatively very leafy as shown by the high leaf/stem ratios (table 2). The early vegetative growth rate and total vegetative growth were greater with 11-hour cool-day plants than with plants grown under southern conditions. There were no consistent differences in the leaf/stem ratios of the two treatments.

[7] Symbols in parentheses refer to treatments outlined in table 1.

FIGURE 4.—Vegetative growth of potato plants under various combinations of day length and temperature, 1934–35: *A–D*, Strains 12 (*a*, *c*) and 23 (*b*, *d*) exposed to 11 (*a*, *b*) and to 16 hours of light (*c*, *d*) in treatments 11C and 16C, respectively. Dates and number of days after emergence when photographs were taken: *A*, November 7, 18 days; *B*, December 8, 49 days; *C*, January 3, 75 days; *D*, January 25, 97 days. *E–H*, Strains 12 (*a*, *d*) 22 (*b*, *e*), and 23 (*c*, *f*) grown under southern (*a–c*) and under northern (*d–f*) conditions. Dates and number of days after emergence when photographs were taken: *E*, November 28, 28 days; *F*, December 22, 52 days; *G*, January 14, 75 days; *H*, February 4, 97 days. Height of plants may be gauged by diameter of the 10-inch pots used. Data secured from strain 22, an intermediate-season line, are intermediate between those for strains 12 and 23, but are not published.

Vegetative growth was very extensive when days were long in the early part of the season as with either 16-hour cool days (16C) or northern conditions (N34, N+, N−) (figs. 5 and 6). With these

conditions there was very little or no more elongation of the main axis than with short-day plants, but there was very extensive growth of laterals from nodes on all parts of the plants and numerous flower clusters developed (fig. 4). The rapid early growth rate continued till shortly after the sixty-second day after which it decreased slightly. The extent to which these 16-hour cool-day plants were less leafy

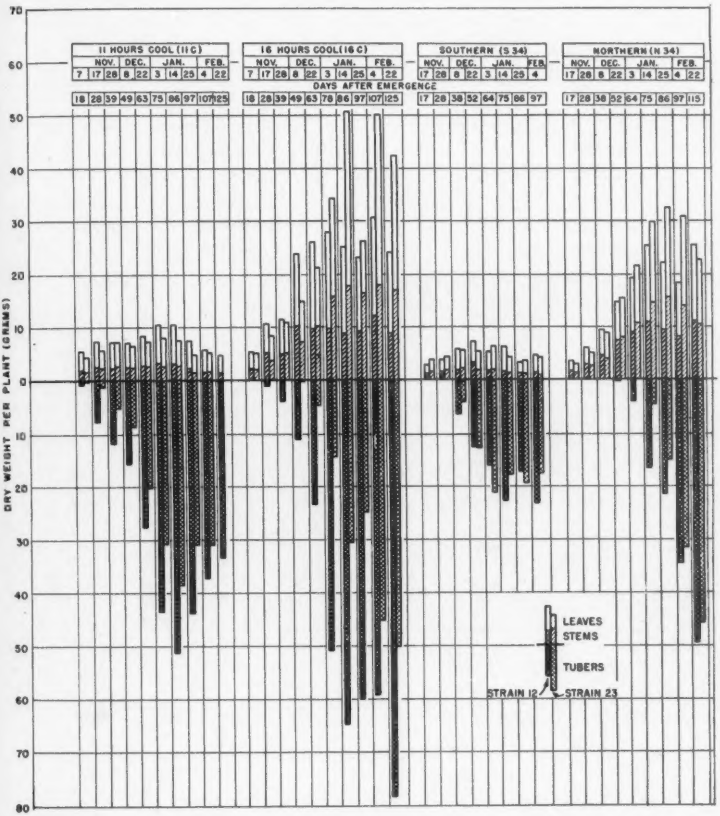

FIGURE 5.—Mean dry weight per plant (in grams) in various parts of plants of two potato strains harvested on successive dates and grown in 1934–35 with 11- and 16-hour cool days (11C and 16C) and under northern and southern conditions (S34 and N34).

than those grown with 11-hour cool or southern days was shown by the very much lower leaf/stem ratios (table 2). These plants matured 15 to 20 days later than the 11-hour-cool or southern-type plants.

In long hot northern days (N34 and N+) the early growth was not exceptionally rapid. Leaf development was proportionately less than with southern-day plants ((S34 and S+), but stem development was greater, as is shown by the dry weights (figs. 5 and 6) and the leaf/stem ratios (table 2).

When a shortage of nitrogen occurred in the nutrient solution vegetative growth was very much inhibited. Under southern conditions the vegetative growth of nitrogen-deficient plants was only about 60 percent of that of plants given a complete nutrient solution (S+, S−, fig. 6). With plants grown with both complete and nitrogen-deficient solutions vegetative growth practically ceased before the

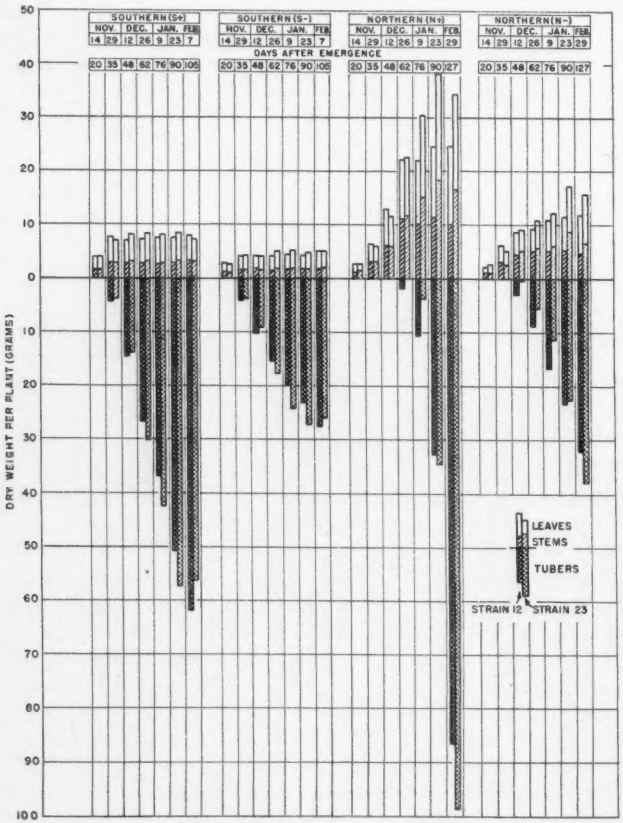
SOUTHERN (S+)
SOUTHERN (S−)
NORTHERN (N+)
NORTHERN (N−)
NOV. DEC. JAN. FEB.
14 29 12 26 9 23 7
14 29 12 26 9 23 29
DAYS AFTER EMERGENCE
20 35 48 62 76 90 105
20 35 48 62 76 90 127
DRY WEIGHT PER PLANT (GRAMS)
50 40 30 20 10 0 10 20 30 40 50 60 70 80 90 100
LEAVES
STEMS
TUBERS
STRAIN 12
STRAIN 23

FIGURE 6.—Mean dry weight per plant (in grams) in various parts of plants of two potato strains harvested on successive dates and grown in 1935–36 under southern and northern conditions with a balanced nutrient solution (S+, N+) and with a nitrogen-deficient solution (S−, N−).

thirty-fifth day, the short cool days having been a greater factor in inhibiting vegetative growth than the absence of nitrogen. This nitrogen deficiency did not alter the leaf/stem ratios. Under northern conditions (N−) the maximum vegetative growth of plants raised on a nitrogen-deficient solution was less than half as great as when nitrogen was applied in abundance N+). Under northern conditions vegetative growth of nitrogen-deficient plants continued until the seventy-fifth day or later. Thus the long warm days early in the

TABLE 2.—*Ratios of dry weight of leaves to stems of strains 12 and 23* [1] *of Triumph potatoes as affected by temperature, day length, nitrogen supply, and time of harvest, 1934–35, 1935–36*

Age of tops when tubers harvested (days)	1934–35								1935–36							
	11-hour cool day (11C) [2]		16-hour cool day (16C) [2]		Southern conditions (S34) [2]		Northern conditions (N34) [2]		Southern conditions				Northern conditions			
									(S+) [2]		(S−) [2]		(N+) [2]		(N−) [2]	
	12	23	12	23	12	23	12	23	12	23	12	23	12	23	12	23
17–20	1.78	1.66	1.38	1.50	1.66	1.68	1.24	1.27	1.88	1.83	1.71	1.88	1.45	1.46	1.34	1.39
28	1.88	1.47	1.11	1.29	1.46	1.38	1.15	.99								
35									1.98	1.79	1.86	1.87	1.32	1.25	1.11	1.11
38–39	1.96	1.49	1.34	1.12	1.29	1.74	1.11	1.13								
48–52	1.71	1.16	1.16	1.08	1.35	2.03	1.23	.97	1.83	2.08	1.80	2.10	1.17	1.00	1.09	.90
	1.90	1.94	1.44	1.10	2.18	2.57	1.17	1.05	2.22	2.26	2.11	2.20	1.11	1.00	1.09	.93
75–76	2.14	1.87	1.60	1.18	2.75	2.42	1.36	1.07	2.52	2.23	2.27	2.10	1.25	1.05	1.34	1.11
86–92	2.28	1.73	1.81	1.38	1.60	2.21	1.38	1.10	2.22	2.11	2.21	2.07	1.27	1.16	1.32	.98
97	2.43	2.75	1.50	1.30	1.38	[3] 3 69	1.29	1.23								
105–107	2.49	2.61	1.50	1.76					1.97	1.85	2.20	1.91				
115 [4]							1.36	1.18								
125–127 [4]	2.18	1.65	1.72	1.52									1.61	1.18	1.75	1.39

[1] 12=very early strain; 23=very late strain.
[2] Symbols in parentheses are treatment identification. For complete statement concerning these treatments see table 1 and pp. —.
[3] Ratio high because of decay of lower stem portions.
[4] Ratios of weights for last 2 harvest periods not entirely dependable because of loss of portions of dead lower leaves by shattering.

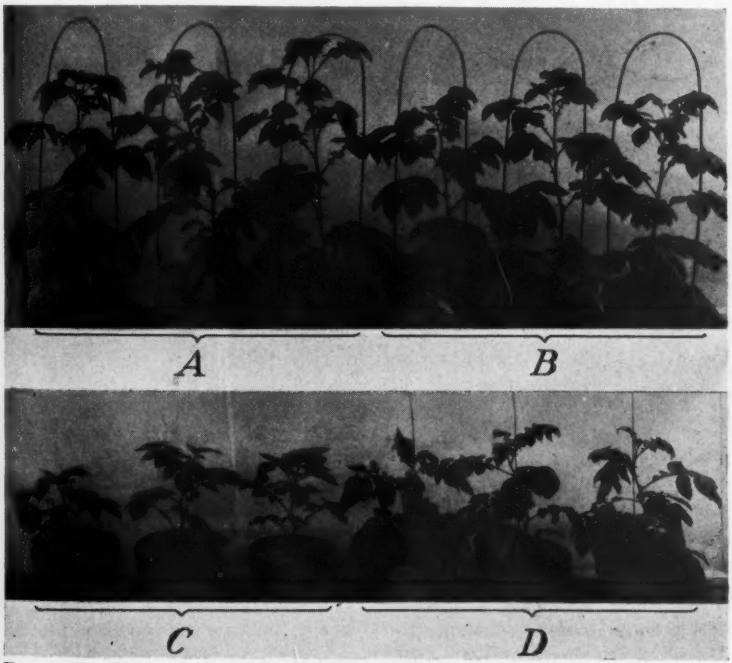

FIGURE 7.—Plants from strain 12 photographed on April 12, 1935, after having been grown for 2 weeks with solutions containing different amounts of nitrogen. Plants of various treatments as designated in table 1 are: *A*, S++; *B*, S+−; *C*, S−−; and *D*, S−+.

season were able to bring about vegetative growth in spite of a serious nitrogen deficiency. However, these nitrogen-deficient northern plants were a trifle less leafy than those receiving a complete balanced solution as shown by lower leaf/stem ratios (table 2).

Under southern conditions when sunlight was good (spring of 1935) decreasing the nitrogen supply 4 weeks after plant emergence resulted in a slight decrease in vegetative growth (S++ to S+−, figs. 7 and 8). When the nutritive solution change was in the other direction

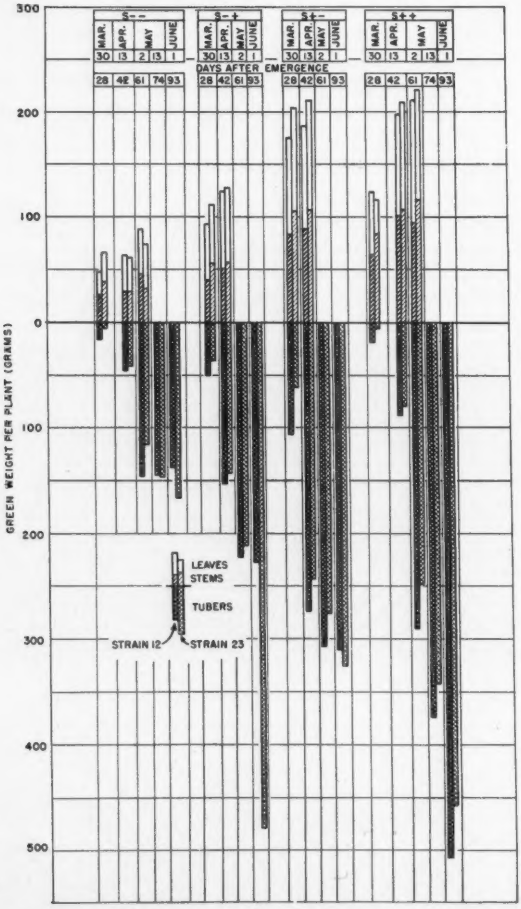

FIGURE 8.—Mean fresh weight per plant (in grams) in various plant parts of plants of two potato strains harvested on successive dates when grown in the spring of 1935 under southern conditions with different amounts of nitrogen in the nutrient solutions. Plants given treatment S−− continually received a nitrogen-deficient solution. At the close of the first 4 weeks the solution given S−+ plants was changed from a nitrogen-deficient solution to a balanced solution and S+− was changed from balanced to a nitrogen-deficient solution. Plants of S++ received a balanced solution continuously.

there was a prompt and significant increase in growth (S− − to S− +, figs. 7 and 8). Following the shift from nitrogen deficiency to abundance there was little or no increase in stem growth, but all leaves were greatly enlarged and changed from a stiff light green to a more flexible dark green. With the shift from an abundance to a deficiency of nitrogen, plants became more compact as a result of the inhibition of stem elongation and the cessation of leaf differentiation. Apparently there was sufficient nitrogen reserve within the plants to supply them for some time so that the reduction in amount of nitrogen in the nutrient solution did not bring about an acute shortage in 33 days. However, with the plants grown the first 4 weeks with a limited amount of nitrogen the increase greatly accelerated growth, but never to the point where it equaled that of plants of either the S+ + or the S+ − series. Plants of these treatments were not dried at harvest time; hence ratios comparable to those of other series could not be calculated.

STOLON GROWTH

Stolon growth of the plants in the several treatments varied greatly in amount, duration, and type. The inhibition or cessation of stolon growth was inseparably associated with the initiation and development of tubers. Short days early in the season always resulted in very small stolon systems consisting of short primary stolons at each of the underground nodes with tubers terminating these stolons within the first few weeks (figs. 9 to 12). Lateral stolons were few and short, and branch stolons occurred very rarely. All nontuberous stolons or stolons bearing small tubers, especially if they occurred at one of the upper nodes, were rapidly resorbed shortly after the thirtieth day. Increasing the day length or temperature, either gradually or abruptly, did not alter the stolon growth of such plants.

When the days were long early in the season the stolon systems were very extensive because of long stolons and numerous lateral and branch stolons. Under northern conditions with the long warm days early, the stolon growth was more extensive than with 16-hour cool days. This was mostly the result of delayed tuberization. Resorption of nontuberous stolons began sometime after the fiftieth day—according to time of tuberization and continued till the end of the season. However, with less or no dominance of a few early-formed tubers more small tubers developed to appreciable size and fewer tuberous stolons appeared to be resorbed than when the growth of a few tubers became dominant, as with the plants having short days early in the season. This lack of dominance was most apparent with northern-condition plants (figs. 10, 13, and 14).

With a low nitrogen supply stolon growth was restricted only a trifle under southern conditions but to a very pronounced extent under northern conditions (figs. 11 to 14). These differences were again closely associated with tuber initiation. Under northern conditions with a nitrogen deficiency (N−, fig. 14) the stolon growth was quite similar to that under southern conditions with a balanced solution (S+, fig. 11). However, with northern nitrogen-deficient plants stolons were longer than with southern plants receiving a balanced solution, and lateral and branch stolons were quite numerous, whereas they were practically absent from the latter. The nitrogen-deficient northern plants also had a considerable number of nontuberous stolons or stolons with very small tubers until the end of

the season. This condition was almost absent from southern balanced-solution plants. This finding is in harmony with other data which have shown northern plants grown with a nitrogen deficiency to be more vegetative than southern plants grown with a balanced solution.

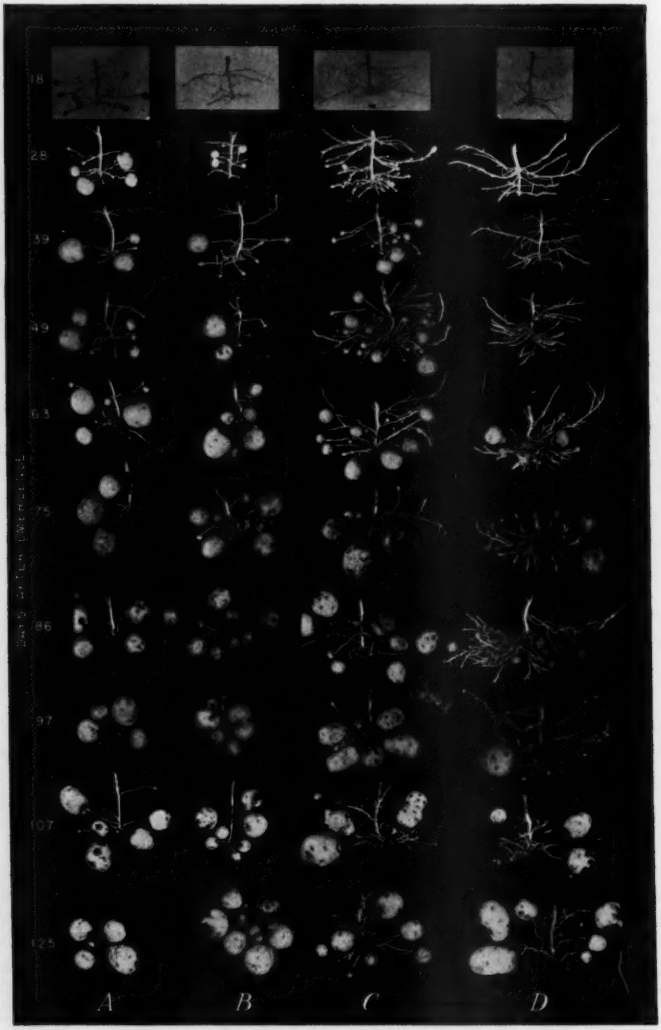

FIGURE 9.—Stolon and tuber production at various harvesting periods by typical plants of two potato strains grown with 11-hour and 16-hour cool days in 1934–35 (11C and 16C). Numbers at left indicate days after emergence: *A*, *B*, Short cool day (11C); *C*, *D*, long cool day (16C); *A* and *C*, strain 12; *B* and *D*, strain 23.

During a period of good sunshine under southern conditions the stolon system of balanced-solution plants differed from nitrogen-deficient plants only in being a trifle longer and in having a few more laterals, all systems being relatively very simple and not altered by nutritional changes made at the close of the first 4 weeks.

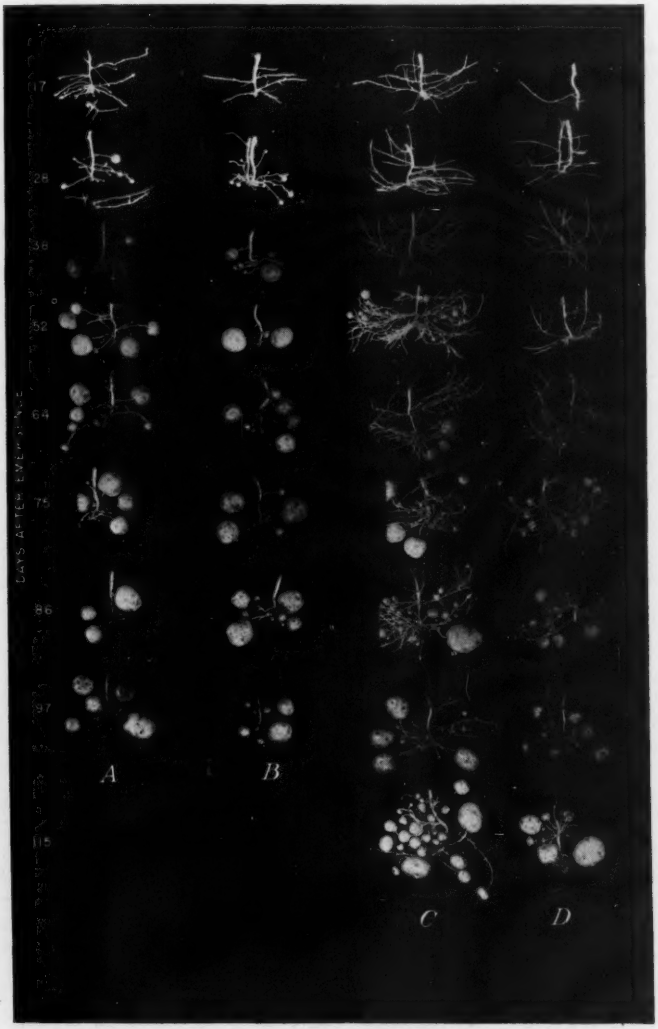

FIGURE 10.—Stolon and tuber production at various harvesting periods, by typical plants of two potato strains grown under southern and northern conditions in 1934–35 (S34 and N34). Numbers at left indicate days after emergence: *A*, *B*, Southern conditions (S34); *C*, *D*, northern conditions (N34); *A* and *C*, strain 12; *B* and *D*, strain 23.

TUBER DEVELOPMENT

The earliest tubers were produced by 11-hour cool-day plants and the latest by northern-day plants. With strain 12 the first tubers were differentiated by the 11-hour cool-day plants about the twelfth day, the southern plants the eighteenth day, the 16-hour cool-day plants a little later, and the northern plants about the forty-eighth day. Nitrogen shortage hastened tuberization at least 2 weeks under northern conditions (figs. 13 and 14) but did not accelerate tuber initiation appreciably under southern conditions (figs. 11 and 12).

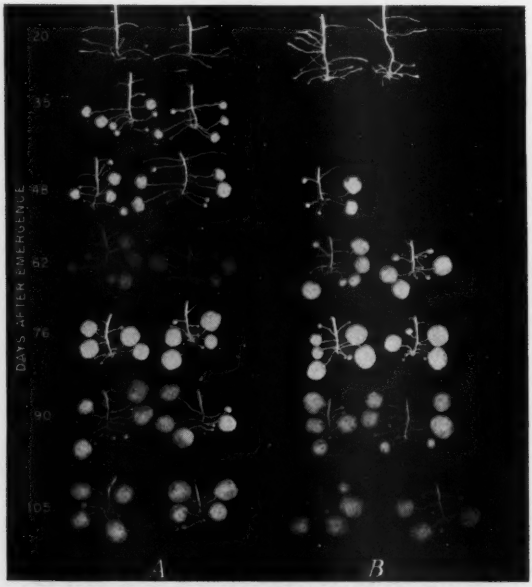

FIGURE 11.—Stolon and tuber production at various harvesting periods by two plants of two potato strains grown under southern conditions in 1935–36 with complete nutrient solution (S+). Numbers at left indicate days after emergence: *A*, Strain 12; *B*, strain 23.

When short, cool days occurred early in the season the first tubers were differentiated from the terminal buds of the primary stolons located at the lower nodes, but at most only a few days elapsed before all primary stolons and all other stolon axes were similarly terminated. With this early tuberization stolon elongation ceased and no new stolon growth occurred. Tuberization was a relatively abrupt process with these short-day plants. The earlier tuberization occurred, the more abruptly did it seem to take place.

When the days in the early part of the season were long, tuberization not only occurred much later than when they were short, but the process was very gradual. With the decreasing day length and declining temperature of the northern conditions tuberization occurred later and again more gradually than with the 16-hour constantly cool days. With these long-day plants the early tuberization generally began at the terminal buds of only a few primary stolons.

Stolon growth reached its peak at about the time of tuberization, even though many stolon buds did not tuberize.

A deficiency of nitrogen in the nutrient solution hastened tuber setting by at least 2 weeks under northern conditions but caused little difference under southern conditions (figs. 12 and 14).

When the days in the early part of the growth period were short, all tubers were set within a comparatively short time early in the season, but when these initial days were long, the process was more attenuated and the maximum number was set later (table 3). The maximum number setting was two to three times greater when early

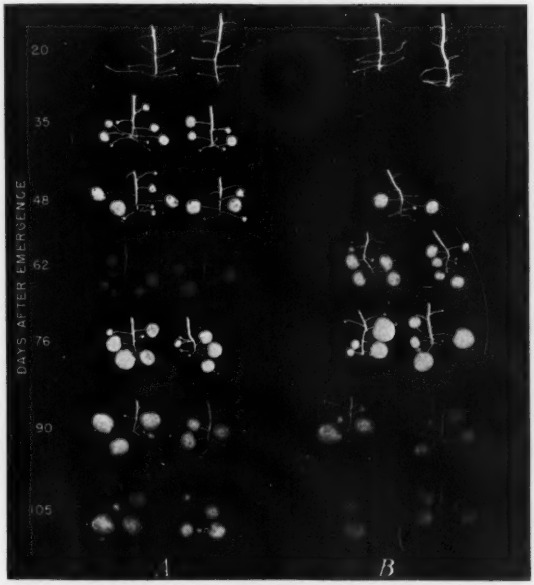

FIGURE 12.—Stolon and tuber production at various harvesting periods by two plants of two potato strains grown under southern conditions in 1935–36 with a nitrogen-deficient solution (S−). Numbers at left indicate days after emergence: *A*, Strain 12; *B*, strain 23.

days were long than when they were short. With both groups the maximum number of tubers occurred at about the same time as did the maximum vegetative weight. With later harvests these maxima in tuber number and vegetative weight both declined. These trends were least defined in the continual cool-day plants. Apparently with the declining plant vigor the smaller tubers were resorbed. The number of tubers weighing more than 1 gm. was also greater with early long- than with early short-day plants.

A deficiency of nitrogen greatly decreased the number of tubers under northern conditions, but under southern conditions the decrease both in total number and in larger tubers was again relatively very much less.

The total yield of tubers and the rate of growth during various periods were very greatly influenced not only by the experimentally altered factors of temperature, day length, and nutrition but also

by the intensity of the natural daylight and by the intensity of light used to extend the natural photoperiod (table 4). The tuber-weight increase was relatively high early in the season with the treatments that had short days early in the season. When the early days were warm and long the greatest tuber-weight increase occurred in the latter part of the season (table 5).

Plants grown with the 11-hour cool days had relatively the most rapid increase during the first 28 days. After that the daily tuber dry-weight production was greater during each succeeding interval till the seventy-sixth day. There was a very slight slowing up of the

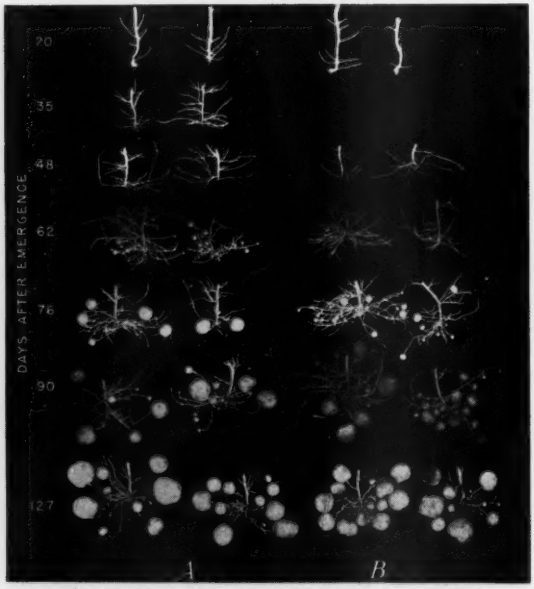

FIGURE 13.—Stolon and tuber production at various harvesting periods, by two plants of two potato strains grown under northern conditions in 1935–36, with a complete nutrient solution (N+). Numbers at left indicate days after emergence: *A*, Strain 12; *B*, strain 23.

tuber increase rate prior to the forty-ninth day when the daylight was the poorest of the season. After the seventy-sixth day tubers continued to increase in weight but at a greatly reduced rate. After the ninetieth day there was a decrease in dry weight of tubers.

The tuber growth rates of the southern plants were relatively rapid early in the season. During periods of low light intensity the growth rate was relatively low (figs. 2 and 3). The tuber growth rates of southern nitrogen-deficient plants were much the same as those of plants grown with balanced solutions except that they showed a more rapid rate of increase early followed by a slower rate of increase (S− and S+).

When days were long and cool early in the season (16C) tuberization was not only later than when days were short and cool (11C) but the very early tuber growth was also a little slower. From the forty-ninth to the seventy-fifth day the growth rate of 16-hour cool-day

plants continued to increase. After the eighty-sixth day the tubers of 11-hour cool- and southern-day plants had stopped growing or were losing weight. The northern plants with their long warm early days were slowest to tuberize. Consequently their period of most rapid relative increase was always a number of days later than that of plants under any other growing conditions. Their rate of increase was still very rapid till the tests were terminated and the plants were beginning to mature.

The tuberization efficiency of a strain or treatment may be judged by the daily dry weight increase of tubers per gram of dry leaf weight.

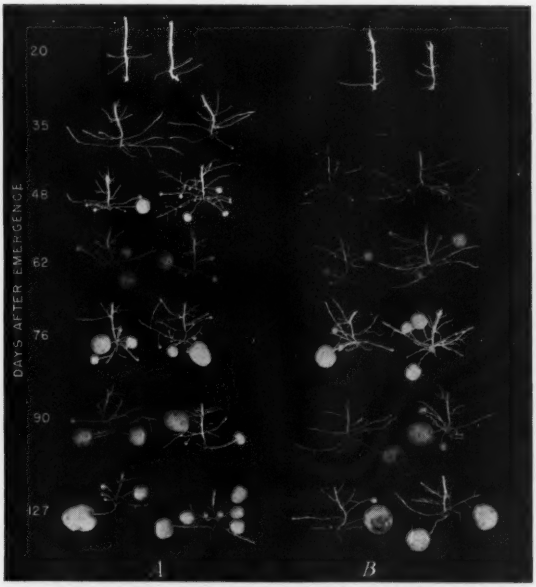

FIGURE 14.—Stolon and tuber production at various harvesting periods, by two plants of two potato strains grown under northern conditions in 1935–36 with a nitrogen-deficient solution (N−). Numbers at left indicate days after emergence: *A*, Strain 12; *B*, strain 23.

On this basis 11-hour cool-day plants were by far the most efficient early in the season (table 5). The southern nitrogen-deficient plants were more efficient during the first 48 days than plants grown with a balanced solution (S−, S+). From then on until the ninetieth day or later the southern plants grown with a balanced solution produced more tuber weight per dry weight of leaves than did the southern nitrogen-deficient plants. With plants under northern conditions tuber production per weight of leaf per day was much lower than for southern plants until very late in the season when the southern plants were maturing more rapidly. Northern nitrogen-deficient plants had a higher rate than balanced-solution plants till after the seventy-sixth day (N+, N−). Then leaves of the nitrogen-deficient plants became yellow or died and were very inefficient during the cool short days at the close of the period, whereas leaves of the balanced-solution plants continued active.

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TABLE 3.—*Mean number of tubers weighing more than 1 gm. and total number per plant, for strains 12 and 23* [1] *of Triumph potatoes, as affected by temperature, day length, nitrogen supply, and time of harvest, 1934–35, 1935–36*

TUBERS WEIGHING MORE THAN 1 GM. PER PLANT

Age of tops when tubers were harvested (days)	1934–35								1935–36							
	11-hour cool day (11C) [2]		16-hour cool day (16C) [2]		Southern conditions (S34) [2]		Northern conditions (N34) [2]		Southern conditions				Northern conditions			
									(S+) [2]		(S−) [2]		(N+) [2]		(N−) [2]	
	12	23	12	23	12	23	12	23	12	23	12	23	12	23	12	23
17–20	3.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	4.5	4.0	3.5	0	4.5	2.5	0	0								
35									5.5	5.2	4.0	3.5	0	0	0	0
38–39	4.5	6.5	7.5	0	4.0	3.3	0	0								
48–52	4.5	3.5	17.0	0	8.0	4.0	3.0	0	5.5	4.8	4.0	3.5	0	0	2.0	0
62–64	6.5	12.0	8.5	3.5	6.7	5.7	4.7	0	6.2	5.7	4.5	4.7	4.5	0	2.7	2.2
75–76	9.0	9.5	6.5	4.5	6.0	5.0	9.0	9.0	5.2	5.5	5.0	4.5	4.7	5.0	2.5	2.5
86–90	8.5	8.0	8.0	6.0	3.3	5.0	8.0	6.6	5.7	6.5	3.8	3.6	6.6	8.2	3.0	2.2
97	6.5	5.0	7.0	3.0	8.0	5.0	8.5	5.5								
105–107	6.0	9.5	9.0	3.0					5.0	5.0	4.5	3.5				
115							13.5	8.0								
125–127	6.0	10.0	8.6	5.3									10.0	11.5	5.2	3.0

TOTAL TUBERS PER PLANT

17–20	15.0	3.3	0	0	8.0	0	0	0	1.0	0.3	2.7					
28	11.0	7.0	17.5	0	15.5	12.5										
35									15.7	15.0	8.2	7.7				
38–39	12.0	12.5	16.0	2.5	18.3	11.5	.0	0							4.5	0
48–52	16.0	9.0	43.5		16.3	15.0	11.7	0	12.7	13.5	7.7	8.5			14.0	6.5
62–64	11.0	15.5	24.5	19.0	15.0	14.0	34.3	0	12.7	12.2	7.5	8.5	39.0	4.8	13.5	7.0
75–76	15.0	15.0	25.0	39.5	10.6	9.0	37.3	27.0	12.5	8.5	7.2	7.5	17.0	24.8	10.2	8.2
86–90	11.5	14.0	24.0	39.0	5.0	10.0	43.6	28.6	9.2	9.5	6.2	7.0	35.0	53.2	9.0	8.7
97	11.5	5.5	21.5	46.0	9.3	8.0	34.5	19.6								
105–107	11.0	9.5	22.0	10.0					9.0	8.0	5.8	6.5				
115							22.0	16.5								
125–127	6.0	11.0	11.3	9.6									26.0	37.0	9.2	5.0

[1] 12=Very early strain; 23=very late strain.
[2] Symbols in parentheses are treatment identification. For complete statement concerning these treatments see table 1 and pp. 761–763.

TABLE 4.—*Mean fresh weight of tubers as grams per plant for strains 12 and 23* [1] *of Triumph potatoes as affected by temperature, day length, nitrogen supply, and time of harvest, 1934–35, 1935–36*

Age of tops when tubers were harvested (days)	1934–35								1935–36							
	11-hour cool day (11C) [2]		16-hour cool day (16C) [2]		Southern conditions (S34) [2]		Northern conditions (N34) [2]		Southern conditions				Northern conditions			
									(S+) [2]		(S−) [2]		(N+) [2]		(N−) [2]	
	12	23	12	23	12	23	12	23	12	23	12	23	12	23	12	23
17–20	6.8	0.1	0	0	0.6	0	0	0.07	0.07	0.03	0.13	0	0	0	0	0
28	64	10	9	0	7	3	0	.0								
35									35	30	34	31	0	0	.6	0
38–39	96	44	31	.4	52	34	0	.0								
48–52	117	67	91	.8	101	96	5.3	.0	107	107	68	65	0	0	26	2.5
62–64	193	159	181	41	114	145	36	.4	177	192	103	114	16	.2	68	45
75–76	343	219	332	115	149	116	133	38	232	256	130	153	108	31	116	85
86–92	306	234	439	212	108	123	156	109	300	328	149	171	217	250	157	148
97	274	186	378	311	151	105	206	187								
105–107	229	214	360	266					363	329	187	180				
115							299	248								
125–127	210		455	298									489	560	209	220

[1] 12=Very early strain; 23=very late strain.
[2] Symbols in parentheses are treatment identification. For complete statement concerning these treatments see table 1 and pp. 761–763.

TABLE 5.—*Increase or decrease in dry weight of tubers, expressed as the mean daily amount in milligrams per plant and per gram of dry leaf, strains 12 and 23* [1] *of Triumph potatoes, as affected by temperature, day length, nitrogen supply, and time of harvest, 1934–35, 1935–36*

PER PLANT BASIS

Age of tops when tubers were harvested (days)	11-hour cool day (11C) [2]		16-hour cool day (16C) [2]		Southern conditions, 1934–35 (S34) [2]		Northern conditions, 1934–35 (N34) [2]		Southern conditions, 1935–36				Northern conditions, 1935–36			
									(S+) [2]		(S−) [2]		(N+) [2]		(N−) [2]	
	12	23	12	23	12	23	12	23	12	23	12	23	12	23	12	23
	Milligrams	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*
17–28	45	1	0	0	3	0	0	0	1	3	2	0	0	0	0	0
28	706	107	106	0	42	33	0	0								
35									285	253	384	262	0	0	4	0
38–39	358	356	257	3	599	378	0	0								
48–52	405	348	715	2	441	620	38	0	783	778	454	399	0	0	225	204
62–64	842	821	889	330	288	714	298	1	885	1,160	367	434	108	0.4	420	377
75–76	1,325	874	2,295	807	605	344	1,155	433	725	878	330	475	629	257	551	417
86–90	1,000	719	1,266	1,473	492	167	459	962	990	1,063	224	208	1,600	2,216	480	789
97	−668	−688	−446	−507	518	167	1,185	1,505								
105–107	−677	4	−49	2,024					735	−63						
115							826	785								
125–127			1,060	2,761							301	94	1,390	1,880	244	420

DRY-LEAF-WEIGHT BASIS

17–20	25	0.5	0	0.0	3	0	0	0.0	0.1	1	1	0	0	0	0	0
28	169	35	24	0	21	13	0	0								
35									22	19	35	32	0	0	1	0
38–39	75	92	42	.6	200	124	0	0								
48–52	87	84	73	.3	105	175	6	0	33	38	45	39	0	0	16	2
62–64	168	187	63	35	70	176	34	.1	47	49	36	38	4	0	24	22
75–76	209	175	141	55	115	90	94	33	35	39	31	37	14	5	26	19
86–90	14	144	76	69	153	61	34	60	46	47	20	17	32	32	20	27
97	−106	−164	−30	−17	200	60	104	89								
105–107	−143	0	−3	62					35	−3	20	−8				
115							67	54								
125–127			63	10									19	25	7	12

[1] 12=Very early strain; 23=very late strain.
[2] Symbols in parentheses are treatment identification. For complete statement concerning these treatments see table 1 and pp. 771–763.

On the basis of dry weight of tubers produced for each gram of leaf and stem dry weight, i. e., tuber/top ratios, the most efficient plants very early in the season were the 11-hour cool-day plants (11C), followed rather closely by the southern plants (S34, S+, S− (table 6)). The ratios with these plants, which it will be remembered had relatively small vegetative growth, remained high all season. The ratios of 16-hour cool-day plants were much lower than those of the 11-hour cool-day plants, but those of northern plants were generally still lower. Early in the season the tuber/top ratios of nitrogen-deficient plants were always higher than those of the corresponding balanced-solution plants, but late in the season they were lower. As vegetative growth increased the tuber/top ratio decreased. The conditions that were most favorable for maximum vegetative growth were least favorable for most efficient tuber production when calculations were made on the basis of a unit of leaf area.

TABLE 6.—*Ratios of dry weight of tubers to that of vegetative parts (tops) for strains 12 and 23* [1] *of Triumph potatoes as affected by temperature, day length, nitrogen supply, and time of harvest, 1934–35, 1935–36*

Age of tops when tubers were harvested (days)	1934–35								1935–36							
	11 hour cool day (11C) [2]		16 hour cool day (16C) [2]		Southern conditions (S34) [2]		Northern conditions (N34) [2]		Southern conditions				Northern conditions			
									(S+) [2]		(S−) [2]		(N+) [2]		(N−) [2]	
	12	23	12	23	12	23	12	23	12	23	12	23	12	23	12	23
17–20	0.14	.....	0.00	0.00	0.17	0.00	0.00	0.00	.....	0.01	0.01	0.00	0.00	0.00	0.00	0.00
28	1.07	0.20	.10	.....	.14	.08	.00	.00								
35									0.57	.50	1.01	.93	.00	.00	.11	.00
38–39	1.64	.72	.29	.03	1.13	.73	.00	.00								
48–52	2.23	1.32	.46	.04	1.75	2.46	.03	.00	2.07	1.60	2.34	2.22	.00	.00	.35	.03
62–64	3.28	2.75	.90	.22	3.06	3.35	.22	.08	3.46	3.41	3.80	3.48	.08	.00	.94	.52
75–76	4.16	3.84	1.84	.42	3.75	4.08	.67	.16	4.57	4.98	4.46	4.64	.49	.12	1.52	.92
86–92	4.87	5.11	2.58	.61	5.47	5.62	1.00	.48	6.36	6.40	5.35	5.49	1.34	.85	2.05	1.29
97	5.86	6.25	2.59	.42	5.06	4.38	1.94	1.05								
105–107	6.33	5.92	1.95	.91	.....	.....	.....	.....	7.28	7.26	5.24	5.04	.....	.....	.....	.....
115					.....	.....	1.96	2.06	.....	.....	.....	.....	.....	.....	.....	.....
125–127	6.85	5.61	3.27	1.18	.....	.....	.....	.....	.....	.....	.....	.....	3.72	3.03	2.70	2.42

[1] 12=Very early strain; 23=very late strain.
[2] Symbols in parentheses are treatment identification. For complete statement concerning these treatments see table 1 and pp. 761–763.

It is of interest to note the comparative merits of the various treatments for total tuber production during given periods of time in various parts of the growing season. Plants that started with cool short days and tuberized early produced a large weight of tubers per plant per day during a 50- to 60-day period, with heavy production under way relatively early (11C, 16C, southern, table 5). When tuberization was once initiated long warm days did not prevent great tuber increase even though they might have prevented or delayed initiation of tubers. With northern plants the maximum tuber production per day was approximately twice as great as the maximum for southern plants that were growing at the same time but this rate was not attained until the seventy-sixth day or later. Prior to the sixty-second or seventy-sixth day the nitrogen-deficient plants under northern conditions (N−) were yielding more per day than the balanced-solution plants. Under southern conditions the

tuber production of nitrogen-deficient plants (S—) was higher than that of balanced-solution plants (S+) till the thirty-fifth day. After that the S— plants produced much less per day than the S+ plants as the leaves were chlorotic and were approaching or had reached senility.

The final yield of tubers was always greater with the plants that had the larger tops. With such large plants production per leaf unit was relatively low (table 5), but the total leaf system was so great that the total tuber production was relatively great. At any time up to about 75 to 90 days after emergence the southern plants were more productive than the northern plants. After that time tuber yields of southern plants increased very little, but from then on half of the tuber weight of northern plants was produced. The production of poorly illuminated southern plants was relatively low, whereas that of well-illuminated plants was finally equal to or greater than that from 11-hour cool-day plants. The 16-hour cool-day plants attained higher early tuber production rates per gram of leaf weight than northern plants but the final production rate was greater with the latter.

A nitrogen deficiency curtailed total tuber production more under northern than under southern conditions. The nitrogen-deficient plants were not able to benefit by the cool short days at the close of the northern season because of the great reduction in leaf area, the reduced amount of chlorophyll, and the early death of the plants. In an experiment conducted in the spring of 1935, when a nitrogen deficiency existed all season under southern conditions final tuber production was about one-third as great as when nitrogen was supplied in adequate amounts all season (S— — and S+ +, fig. 8). Increasing the nitrogen supply from the nitrogen—deficient solution to a complete solution (S— +) at the end of 2 weeks brought about a great increase in yield. Decreasing the amount of nitrogen at the end of 4 weeks (from the complete solution to the nitrogen-deficient solution) resulted in about a 30-percent reduction in tuber yield (S+— as compared with S+ +). However, this yield was still greater than when nitrogen was deficient only early in the season (except with strain 23). Stated differently, this means that with the early strain under southern conditions a high nitrogen supply for 4 weeks early in the season was worth considerably more for tuber production than a high nitrogen supply during the last 8 or 9 weeks, whereas the late strain was able to survive this early deficit and respond to the later abundantly supplied nitrogen. In fact the late strain (23) yielded slightly more with the S— + solution than with the S+ + solution.

Under southern conditions tubers were more uniform, larger, and of better type than under northern conditions (figs. 10 to 14). Under northern conditions a few tubers may have been larger but there was more variation in tuber size than with southern plants. With continually cool days tubers were larger than with other treatments—the largest and most elongated having been produced by 16-hour cool days (fig. 9). When nitrogen was deficient the size of southern tubers was less than when nitrogen was abundant, but the range in size was about the same (figs. 11 and 12). Under northern conditions with a nitrogen deficiency one or two tubers generally grew to great size while the others remained relatively small (fig. 14).

DRY MATTER CONTENT OF VARIOUS PLANT PARTS

The percentage of dry matter in the leaves of both the 11-hour and the 16-hour cool-day plants was relatively high at the time of the first harvest (table 7). After that the percentage of dry matter decreased till about the thirty-ninth day, after which it increased gradually with a very rapid increase as the plants became senile. With southern and northern plants the initial high percentage was less apparent. During all the time prior to the period of senility the percentage in the leaves of 16-hour plants was higher than in those of 11-hour plants. During the first 60 days the dry-matter percentage was greater in the leaves of northern than in those of southern plants.

TABLE 7.—*Percentage of dry matter in leaves, stems, and tubers of strains 12 and 23* [1] *of Triumph potatoes, as affected by temperature, day length, nitrogen supply, and time of harvest, 1934–35, 1935–36*

DRY MATTER IN LEAVES

Age of tops when tubers were harvested (days)	11-hour cool day (11C) [2]		16-hour cool day (16C) [2]		Southern conditions, 1934–35 (S34) [2]		Northern conditions, 1934–35 (N34) [2]		Southern conditions, 1935–36				Northern conditions 1935–36			
									Complete nutrient solution (S+) [2]		Nitrogen-deficient solution (S−) [2]		Complete nutrient solution (N+) [2]		Nitrogen-deficient solution (N−) [2]	
	12	23	12	23	12	23	12	23	12	23	12	23	12	23	12	23
	Per cent	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*
17–20	9.8	9.6	10.1	9.7	7.2	7.3	8.0	7.5	8.6	8.7	8.3	7.6	8.9	8.6	8.1	7.8
28	7.5	7.6	9.3	8.2	7.2	7.2	7.3	6.9								
35									8.1	8.3	7.1	7.2	9.0	8.7	8.1	7.7
38–39	7.4	7.2	8.0	8.1	8.0	8.3	8.4	9.6								
48–52	7.8	7.8	8.8	8.9	7.9	7.7	9.0	8.0	6.6	7.8	6.7	7.1	9.2	9.2	8.8	8.6
62–64	7.7	7.2	8.8	8.7	9.8	9.5	10.9	10.4	7.2	7.5	6.2	6.3	9.6	8.6	7.7	8.0
75–76	8.5	7.7	10.4	9.7	12.4	10.2	12.0	10.0	8.4	7.2	6.3	6.1	11.8	10.3	8.8	9.0
86–90	10.9	9.7	10.3	9.9	13.6	11.2	13.3	11.3	9.6	9.7	7.1	6.7	12.4	11.6	9.9	10.0
97	13.9	11.3	11.9	12.6	33.9	38.1	16.0	12.1								
105–107	23.6		19.9	19.2					39.7	37.2	22.7	21.8				
115							29.4	17.9								
125–127	81.4	81.6	73.9	48.6									17.0	32.7	22.5	13.4

DRY MATTER IN STEMS

17–20	4.5	5.1	4.6	4.6	4.9	4.1	3.9	3.6	3.8	3.9	3.9	3.6	3.6	3.6	3.7	3.6
28	4.5	4.0	5.2	4.0	3.9	4.0	3.8	3.7								
35			.0	.0					3.8	3.9	4.0	3.9	3.9	4.1	4.7	4.4
38–39	4.0	5.3	4.5	4.1	4.2	4.8	4.2	4.4	3.9	3.9	4.0	3.7	4.2	4.2	5.1	5.5
48–52	4.2	4.4	4.8	4.7	6.5	4.4	4.7	4.6								
62–64	4.2	4.3	4.8	4.9	4.7	4.3	4.9	5.0	3.8	3.9	4.0	3.8	4.8	4.5	5.4	5.7
75–76	4.5	4.6	5.1	5.2	4.2	4.9	4.9	5.0	3.7	3.7	4.0	4.1	4.9	5.1	5.4	6.0
86–90	4.5	4.3	5.2	5.2	6.5	4.9	5.1	6.1	3.9	4.2	4.3	4.6	5.1	5.6	5.8	7.2
97	4.8	4.6	5.4	6.2	5.9	5.9	5.7	5.4								
105–107	5.1	17.5	6.4	6.1					5.2	10.8	10.9	7.8				
115				.0			7.4	6.5								
125–127	26.3	59.4	19.0	9.1									5.5	10.4	6.9	8.2

DRY MATTER IN ALL TUBERS

17–20	11.8	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
28	12.3	11.6	11.8	.0	7.9	10.9	.0	.0								
35									12.4	12.6	12.5	12.9	.0	.0	11.6	.0
38–39	12.3	11.7	12.4	10.0	12.5	12.4										
48–52	13.6	12.8	12.1	7.3	12.6	13.4	10.0	.0	13.6	13.0	15.0	14.1	.0	.0	11.6	10.9
62–64	14.3	12.7	13.0	11.4	14.1	14.8	11.6	4.6	15.2	15.7	14.9	15.5	11.9	3.6	13.0	12.4
75–76	16.3	13.9	15.4	12.5	15.3	15.2	12.7	12.6	16.0	16.6	15.3	15.9	12.9	11.6	14.3	13.4
86–90	16.8	16.5	14.8	14.4	16.2	15.8	14.1	14.2	16.9	17.5	15.5	15.9	15.3	13.9	14.8	15.2
97	16.0	16.7	15.9	16.1	15.3	16.8	16.9	17.1								
105–107	16.2	14.5	16.5	17.0					17.0	17.1	14.8	14.4				
115							16.6	18.5								
125–127	15.9		17.3	16.8									18.8	18.6	15.5	17.2

[1] 12=very early strain; 23-very late strain.

[2] Symbols in parentheses are treatment identification. For complete statement concerning these treatments see table 1 and pp. 761–763.

The percentage of dry matter in the stems tended to increase as the season advanced. The percentage in the 16-hour cool-day plants was generally higher than in the 11-hour plants and in the northern than in the southern plants.

With all treatments the percentage of dry matter in the total tuber crop increased rather steadily as the season advanced, but frequently decreased at the time of the last harvest (table 8). This increasing percentage of dry matter was associated with constantly increasing tuber size—the larger tubers consistently having the higher dry-matter percentages (table 8).

TABLE 8.—*Percentage of dry matter in tubers of strains 12 and 23* [1] *of Triumph potatoes, as affected by tuber weight, temperature, day length, nitrogen supply, and time of harvest, 1935–36*

Tuber weight range at harvest and period elapsed since emergence (days)	Southern conditions, 1935–36				Northern conditions, 1935–36			
	Complete nutrient solution (8+) [2]		Nitrogent-deficient solution (8−) [2]		Complete nutrient solution (N+) [2]		Nitrogen-deficient solution (N−) [2]	
	12	23	12	23	12	23	12	23
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
0.01 to 1 gm.:								
20	19.23	16.53	21.15					
35	12.03	11.85	13.30	12.78		11.56		
48	6.86	7.54	9.52	7.58		8.92		10.86
62	8.57	6.88	10.09	11.91	11.90		7.20	7.08
76			11.05	6.73	7.28	11.81	3.51	5.58
90	8.21	8.24	6.57	9.87	7.02	5.81	4.21	4.32
105	10.00	7.10	14.38	3.89				
127					7.76	5.00	7.65	5.00
1.01 to 25 gm.:								
35	12.36	12.61	12.50	12.87				
48	13.60	12.89	14.21	14.40			11.80	
62	12.94	19.89	14.65	15.67	11.82		13.03	12.18
76	13.65	15.34	14.68	16.55	12.29	11.61	13.20	11.89
90	13.82	14.04	14.77	11.44	14.62	13.41	13.02	11.49
105	14.59	16.60	14.60	14.04				
127					16.65	14.48	10.70	7.78(?)
25.01 to 75 gm.:								
48	13.68	13.17	15.43	13.82			11.99	
62	15.33	15.27	15.06	15.44			13.07	12.64
76	16.13	17.76	15.43	16.20	13.33	11.40	14.92	13.48
90	16.57	17.94	15.67	15.44	16.30	14.28	14.13	14.28
105	16.60		14.70	14.23				
127					18.39	18.60	15.75	
75.01 to 150 gm.:								
62	16.10	16.04						
76	15.97	16.44		15.39			14.59	13.97
90	17.40	17.35	15.43	16.54	15.40	14.17	15.52	15.89
105	17.38	17.19	15.07	14.79				
127					19.25	20.65	0	16.45
150.01 gm. or more:								
90								14.44
105								
127					20.09	19.01	16.54	17.85

[1] 12=Very early strain; 23=very late strain.

[2] Symbols in parentheses are treatment identification. For complete statement concerning these treatments see table 1 and pp. 761–763.

On all except the latest harvest dates the tubers of the plants that set the earliest tubers had the highest percentages of dry matter. Those from 11-hour cool days and southern conditions had the high percentages, those from 16-hour cool days were intermediate, and those from northern plants were lowest in dry-matter percentage. The early-harvested tubers from nitrogen-deficient plants had higher percentages than tubers from balanced-solution plants but late in the season they had lower. At the last harvest time the northern 16-hour cool-day tubers and tubers from northern high-nitrogen

plants had the highest percentages. These differences are the result of the great differences on any date in the size and physiological age of the tubers produced under various conditions. The tubers of the early short-day plants were always more mature and uniformly larger than those of early long-day plants just as tubers of nitrogen-deficient plants were more mature than those from balanced-solution plants, especially under northern conditions. When tubers of about the same physiological age are compared the differences are found to have been very slight.

With 11-hour cool-day and southern plant tubers the percentage of dry matter increased very slowly after midseason and sometimes it decreased slightly. Probably some of the dry matter was being dissipated from the tubers by their own respiration at the high temperatures prevailing late in the life of southern-day plants or in the life processes of the senile plants as they lingered on. The high dry matter in northern tubers late in the season was probably the result of the absence of practically all demands for materials for growth and the greatly reduced rate of respiration of plants and tubers. As a result of all of these conditions there was a great increase in surplus carbohydrates, and general rapid tuber enlargement resulted. The lower percentage of dry matter in the late nitrogen-deficient tubers is attributed to the weak condition of the plants during a prolonged period.

STARCH CONTENT OF TUBERS

Analysis of tubers of different size selected from various treatments on several dates in 1935–36 showed a rather definite tendency for starch content to increase as tuber size increased (table 9). When com-

TABLE 9.—*Percentage of starch (fresh basis) in tubers of strains 12 and 23*[1] *of Triumph potatoes as affected by tuber weight, temperature, day length, nitrogen supply, and time of harvest, 1935–36*

Period elapsed since emergence and tuber weight range at harvest (grams)	Southern				Northern			
	Complete nutrient solution (S+)[2]		Nitrogen-deficient solution (S−)[2]		Complete nutrient solution (N+)[2]		Nitrogen-deficient solution (N−)[2]	
	12	23	12	23	12	23	12	23
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
48 days:—1.01–25	6.60							
62 days:								
1.01–25			9.27	11.09			7.56	
25.01–75	9.29						7.53	
75.01–150	10.74							
76 days:								
1.01–25			10.28				7.91	
25.01–75	10.54		11.03					
75.01–150	10.56						10.12	
90 days:								
25.01–75	12.40	11.59	11.27	10.68	11.34	9.40	9.88	
75.01–150	11.51	11.71	10.71	11.68	9.47	9.13		10.69
150+								9.56
105 days:								
1.01–25	9.00							
25.01–75	11.37		9.87	9.85				
75.01–150	11.74		10.46	10.12				
150+								
127 days:								
1.01–25					10.20		6.92	
25.01–75					11.47		11.24	
75.01–150					13.20	13.96		11.04
150+					14.55	13.43	11.43	12.37

[1] 12=Very early strain; 23=very late strain.

[2] Symbols in parentheses are treatment identification. For complete statement concerning these treatments see table 1 and pp. 761-763.

parisons are made with data from tubers of the same size group, harvested on the same early dates, those from southern plants appear to have had more starch than those from northern plants, but, conversely, on late dates the northern tubers had the higher percentage. However, when tubers of the same physiological age are compared these differences are not very great. It appears that tubers of the same size and same physiological age, or harvested from plants of the same physiological age, have approximately the same percentage of starch and dry matter.

COMPARISON OF RESPONSE OF TWO STRAINS

When conditions were very favorable for extensive vegetative growth, as northern (N34, N+) or with 16-hour cool-days (16C), plants of strain 12 (the first early strain) were frequently largest early in the season but genetic limitations came into play and inhibited the growth of this strain rather abruptly during the early midseason period, bringing on the early death of the plants. With strain 23 (the very late strain) these factors came into play later and more slowly so that the vegetative growth of 23 was greater. Under conditions restricting vegetative growth (southern and 11-hour cool) top growth of strain 23 was only slightly greater or was less than that of strain 12. With a nitrogen deficiency, plants of strain 23 were slightly larger than those of strain 12, responding about as with a complete nutrient solution (figs. 4, 5 and 6).

Plants of strain 12 were always more compact, having noticeably shorter internodes, larger leaves, and leaflets and more and larger folioles (fig. 4). These differences recorded as leaf/stem ratios were very pronounced when the size of the plants of strain 23 exceeded that of strain 12 as with northern or cool 16-hour days (table 2). With southern conditions or nitrogen-deficient nutrition the difference in leafiness was less apparent.

Thus it appears that when conditions were unfavorable for vegetative growth or differentiation early in the season, there was little difference in the growth of the two strains. When conditions in the early part of the season were very favorable for vegetative growth the plants of the late strain grew to be very large, owing to prolongation of growth and differentiation and not to more rapid early growth.

Under all conditions the stolon growth got under way somewhat quicker with strain 12 and was more extensive with this strain until tuberization set in (figs. 9 to 14). After that stolon growth was most extensive on strain 23 until it too set tubers. Whenever stolon growth was very extensive as under northern (N34, N+) or 16-hour cool days (16C) the development of stolons of strain 23 lagged rather far behind that of strain 12, but when early days were short (11C, S+, S34) or plants were grown with a nitrogen deficiency (S− or N−) there was very little difference (figs. 9 to 14).

Tuberization always occurred earlier with strain 12 than with strain 23. With 11-hour cool or southern days it occurred very early with little difference between the strains. When tuberization occurred late, as with northern days, the difference between strains was about 16 days, and with 16-hour cool days it was about 25 days. When a nitrogen deficit existed there was little difference between strains in time of tuber setting.

Strain 12 generally set most tubers per plant with southern or 11-hour cool days (table 3). Under northern conditions and 16-hour cool days strain 12 had most tubers early in the season and strain 23 had most in the latter part (except 1934–35 northern). Whenever the number of tubers of 23 exceeded those of 12 it was because of

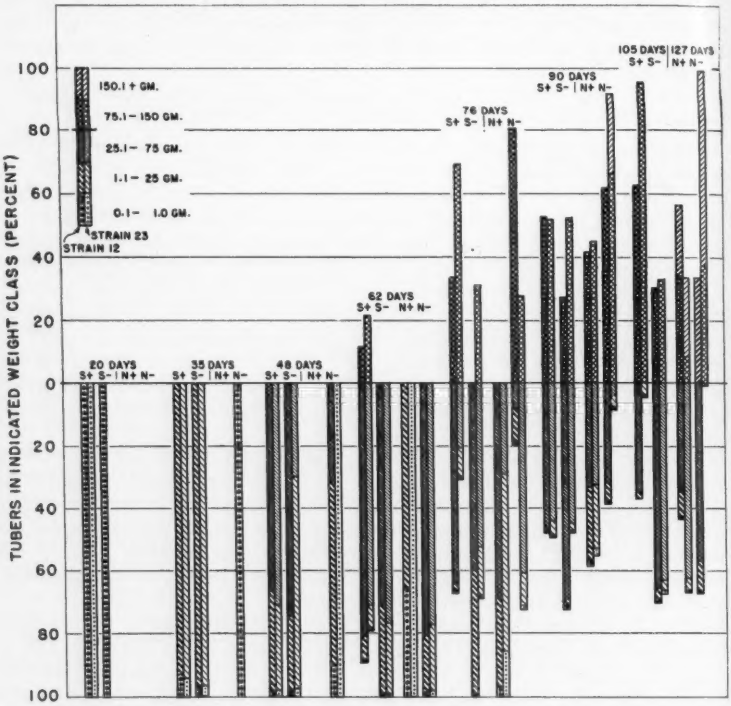

FIGURE 15.—Percentage of total fresh weight of tubers in various tuber-weight classes when harvested the indicated number of days after plant emergence, 1935–36. Letters S and N indicate northern or southern conditions; + and − signs indicate when nutrient solution was balanced or deficient in nitrogen. See table 1 for further information concerning treatments. The two classes of largest tubers are shown in percentage above the zero line, the other classes below.

many tubers having been set late in the season. With a nitrogen deficit there was little difference between strains in number of tubers under southern conditions, but under northern conditions 23 always had fewer.

With both strains many small tubers were resorbed after a peak in numbers had been attained. This peak occurred earlier with 12 than with 23, the difference in the time of peak occurrence corresponding approximately with the difference in time of tuber initiation. The number of tubers weighing in excess of 1 gm. was generally greater with 12 than with 23, although late in the northern season 23 had more in 1935–36.

In the 1935–36 series a higher percentage of the final total weight

of strain 23 occurred in the large-tuber groups than in strain 12 (fig. 15). Most large tubers of strain 12 were nearly of the same size, and none grew to be very large, whereas in strain 23 one or two tubers were much larger than the others. With strain 12 all tubers were set within a very short time; with strain 23 tuberization was a trifle more gradual, and slightly fewer were set.

The total production of tuber dry weight of strain 12 exceeded that of strain 23 at all early harvest periods with all treatments (fig. 5 and table 4) and weights of tubers continued to be highest with strain 12 in the lots that were constantly cool (11C, 16C). Under northern conditions they continued to be greatest until very late in the season. Under southern conditions yields after midseason were most frequently greatest with strain 23 with either type of nutrition, but they were too variable to permit any positive deduction. The most striking difference was in the ability of plants of strain 23 to eventually respond much more than those of strain 12 to a liberal nitrogen supply after the 30-day initial starvation period, as shown in treatment S−+ (fig. 8).

Plants of strain 12 were somewhat more efficient in tuber production than those of 23, having very generally had higher tuber/top ratios (table 6). Under southern conditions there was less difference in these ratios than under northern or continually cool conditions. The relative lack of adaptation of strain 23 to 16-hour cool-day conditions is brought out by the extremely low tuber/top ratio of strain 23. Again it is evident that when conditions are adverse for extensive vegetative growth early in the season or all the season, environmental conditions almost obliterate genetic differences in tuberization habits.

The mean daily tuber production is a means of measuring tuberization capacity at various periods. Under all conditions the daily rate was greater early in the season with strain 12 than with strain 23 (table 5). With strain 12 the maximum production rate was attained earlier in the season and more quickly after tuberization set in than with strain 23.

On the basis of milligrams of dry tuber weight per gram of dry leaf weight per day the rates were always highest for strain 12 very early in the season (table 5). They continued to be highest with strain 12 under northern conditions till very late in the season. Under southern conditions they were highest with strain 23 in the midseason period.

After analyzing the data in various ways it appears that under southern conditions strain 23 was most frequently capable of producing a slightly greater weight of tubers in midseason and later (table 5). This was probably due to the ability of the plants to remain green a little longer than those of strain 12.

On any one date the percentage of dry matter in tubers was generally higher for strain 12 than for strain 23, but this was due to differences in physiological age and size of tubers (tables 7 and 8). On any one date differences were least when tubers of both strains were nearly of the same size and age as under southern conditions or with a nitrogen deficiency. With tubers of the same weight groups the dry matter percentage was sometimes highest with strain 23, probably because of the tendency for the tubers within the group to be larger than with strain 12.

There was little difference in starch content of the tubers from the two strains and any differences observed occurred in the same manner as the dry-matter differences (table 9).

SUMMARY AND CONCLUSIONS

PLANT RESPONSE

A. Triumph potato plants grown in 11-hour cool days produced very small plants, with very high leaf/stem and tuber/top ratios. These plants set tubers very early on a few short stolons. The daily increase in tuber weight per plant or per gram of dry weight of leaves was very great in the early part of the season, but there was no increase after about the seventy-fifth day. The tubers had a relatively high dry-matter content.

B. Plants grown in cool 16-hour days differed from those grown in cool 11-hour days as follows:

(1) Plants were much larger and continued to grow several weeks longer.

(2) Plants were less leafy as shown by lower leaf/stem ratios.

(3) Tuber production occurred several weeks later; tubers were more numerous and were produced on longer stolons.

(4) Total tuber weight was about the same by the time maximum weight was attained by 11-hour plants, after which tuber production continued to increase with 16-hour plants till finally t was approximately twice as great.

(5) The tuber/top ratios were always much lower.

(6) The daily increase in tuber dry weight per weight of leaves was much lower till after midseason.

(7) Dry-matter content of vegetative parts was usually greater; dry-matter content of tubers from plants of the same age was about the same.

C. Plants were produced under "southern" conditions, that is, days increased gradually in length and temperature from short cool days early to long warm days late in the season, and under "northern" conditions with long warm days early and cool short days late. Under southern conditions the response of the plants was very similar to that of 11-hour cool-day plants, whereas under northern conditions the response was similar to that of 16-hour cool-day plants.

D. The southern plants differed from the 11-hour plants in the following respects:

(1) Plants were smaller.

(2) Tuberization occurred a trifle later.

(3) The number of tubers was a trifle smaller.

(4) Tuber weight was considerably lower.

(5) The tuber/top ratios were slightly lower.

E. The northern plants differed from the 16-hour cool-day plants in having:

(1) Less top growth.

(2) Slightly lower leaf/stem ratios.

(3) Much later setting of a greater number of tubers which weighed considerably less.

(4) Lower tuber/top ratios (except late in the season with the very late strain 23).

F. Plants grown under northern conditions differed from those under southern conditions in having:

(1) Much greater vegetative growth, vegetative parts eventually having weighed two to six times more.

(2) Much lower leaf/stem ratios.

(3) Many more tubers which appeared 30 to 40 days later on stolons which were much longer.

(4) Low rate of daily tuber increase per plant before midseason and a very high rate during the last few weeks.

(5) A much lower daily increase per gram of dry weight in leaves and consequently very much lower tuber/top ratios.

(6) Higher dry-matter content in vegetative parts, especially as plants became older.

(7) Probably a slightly greater starch content of tubers.

G. Plants grown with a nutrient solution the nitrogen content of which was only 10 to 20 percent of that in a "complete" nutrient solution differed from those grown with the complete solution as follows:

(1) Vegetative growth was greatly restricted. Under southern conditions increase in vegetative weight practically ceased about the fiftieth day, but under northern conditions it continued 4 to 5 weeks longer. Eventually the decrease in vegetative growth was greater under northern than under southern conditions.

(2) Leaf/stem ratios were generally slightly lower.

(3) Tuber setting occurred much earlier under northern but only slightly earlier under southern conditions.

(4) The number of tubers was greatly reduced, especially under northern conditions.

(5) The yield of tubers on all except the first two harvest dates was much smaller under southern conditions, but under northern conditions it was much greater till after the seventy-sixth day.

(6) Tuber/top ratios were higher till the sixty-second day with southern and till after the ninetieth day with northern plants.

(7) The percentage of dry matter was lower in all comparable plant parts.

(8) Starch content of tubers appeared to be slightly lower.

H. Under the light conditions of early spring at latitude and temperatures typical of the extreme Southern States, reduction in nitrogen at the end of 30 days resulted in a slight reduction in vegetative growth and a brief acceleration of tuberization but finally in a great reduction in yield. Increasing the nitrogen content of the nutrient solution from 20 percent to 100 percent (complete solution) resulted in great increases in vegetative growth and tuber production.

DIFFERENTIAL STRAIN RESPONSE

Under practically all conditions the vegetative growth of the very early strain of Triumph potato was slightly greater than that of the very late strain during the first several weeks after emergence. When conditions were favorable for vegetative growth early or throughout the season the growth of the late strain was greater, but if early conditions inhibited vegetative growth there was little difference between strains after the first few weeks. When an external shortage of nitrogen occurred under any conditions total vegetative growth was most extensive and prolonged with the late strain.

Plants of the early strain were always most leafy and compact as shown by higher leaf/stem ratios.

Stolon growth got under way most quickly with plants of the early strain but generally was most extensive with plants of the late strain.

The first tuber formation took place earliest with the early strains. Under southern, short-day, or nitrogen-deficient conditions this difference was much less pronounced than under northern and long-day conditions or with a complete nutrient solution. Prolongation of vegetative growth appeared necessary to enable the late strain to set more tubers than the early strain.

Prior to midseason the weight of tubers was always greatest with the early strains but there was little difference in final yield. When conditions became very favorable for tuberization late in the life of the plants, as under northern conditions or with the application of nitrogen to starved plants, the yields of the late strains were greatest.

Early-strain plants were most efficient in tuber production as shown by higher tuber/top ratios and greater tuber production per day per gram of leaf weight.

On the basis of the results reported in this paper it is evident that periodic harvesting of plants produced under conditions so controlled as to simulate different combinations of environmental conditions is an effective and dependable means of analyzing strains or varieties with a view to determining their probable performance or suitability in certain regions. With a relatively few plants in a comparatively few months it has been possible to discover the essential differences in strains of Triumph potatoes with more certainty than would have been possible in several years of field tests conducted at numerous points in the United States. The results indicate that intrinsic differences between strains are much less evident or important in southern localities where the conditions early in the season are extremely favorable for tuber development than in northern late-potato regions where the plants start their growth in the hot midsummer days.

LYGUS BUG DAMAGE TO ALFALFA IN RELATION TO SEED PRODUCTION [1]

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INTRODUCTION

Investigations have shown that many factors affect seed setting in alfalfa (*Medicago sativa* L.). No fully satisfactory explanation, however, has been found to account for the major declines in yields of alfalfa seed and the seed-crop failures that have occurred in widely separated regions in recent years. Exceptionally high yields, ranging from 400 to 1,000 pounds or more of seed to the acre, have been reported for earlier years of production in the Arkansas Valley of Colorado and in the Uinta Basin and Millard County of Utah (*1*, *4*).[3] In 1925 Utah produced 22 million pounds of alfalfa seed, which was approximately 40 percent of the Nation's total of that year. This peak in production was followed by a decline in acre yields and a low total production, which since 1930 has frequently not exceeded 5 million pounds annually.

The general decline in yield of alfalfa seed in Utah appears to be partly attributable to bud damage and flower fall that have recently been shown to result from injury caused by *Lygus* bugs (*Lygus hesperus* Knight and *L. elisus* Van Duzee). *L. elisus* was early recognized by McGregor (*8*) as a pest of cotton in California and as having occurred on alfalfa as an alternate host. The *Lygus* problem in alfalfa-seed production has been studied by Sorenson (*10*), who has contributed a knowledge of the biology and life history of *Lygus* in alfalfa under Utah conditions. Stitt (*11*) likewise has made an investigation of the occurrence and activities of *Lygus* in relation to alfalfa-seed production in Arizona. The present investigation was conducted in an attempt to determine the nature of *Lygus* damage to alfalfa and to obtain evidence of the importance of these insects in relation to a rapid decline in alfalfa-seed production in several formerly highly productive regions of the Western States.

[1] Received for publication July 31, 1940. Cooperative investigations of the Division of Forage Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, the Utah Agricultural Experiment Station, and the Wisconsin Agricultural Experiment Station. The material presented here is based on a thesis submitted to the Graduate School of the University of Wisconsin in partial fulfillment of the requirements for the degree of doctor of philosophy.

[2] The author gratefully acknowledges the helpful suggestions of O. S. Aamodt, formerly head of the Department of Agronomy, University of Wisconsin (now head agronomist in charge, Division of Forage Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture), and other members of the staff of the University of Wisconsin; the assistance of D. C. Cooper, assistant professor of genetics, University of Wisconsin, in the histological studies; and the assistance of Fred R. Jones, senior pathologist, Division of Forage Crops and Diseases; C. J. Sorenson, associate entomologist, Utah Agricultural Experiment Station; L. L. Stitt, junior entomologist, Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture; and C. H. Wilkinson, manager, Peppard Seed Co., Delta, Utah. Appreciation is expressed to Eugene Herrling, of the Wisconsin station, and D. F. McAlister, of the Division of Forage Crops and Diseases, for assistance in preparing the photographs.

[3] Italic numbers in parentheses refer to Literature Cited, p. 815.

TYPES OF BUD AND FLOWER DAMAGE IN ALFALFA

SYMPTOMS OF LYGUS DAMAGE

Severe bud damage and flower fall in alfalfa that are attributable to *Lygus* infestation are indicated in the field by whitish-yellow areas or strips that are conspicuous in contrast to the normal deep green of undamaged and healthy alfalfa. The discoloration results from the presence on the plants of dead, dried, and bleached buds and numerous rachises from which flowers have fallen. The symptoms of damage vary with the age of the alfalfa and with the intensity and time of the infestation. New growth under heavy *Lygus* infestation is often noticeably retarded. Stems are sometimes unusually short and thick and may be terminated by a cluster or rosette of many small and distorted racemes of buds. Heavy and prolonged infestation of older growth may frequently result in an appearance of "stringiness" of the plants, due to excessive branching and leafiness that develop from profuse proliferation. In fields that have been recently irrigated or in areas of a field where the growth for some reason is exceptionally rank and succulent, alfalfa appears to be particularly susceptible to this damage when heavily infested with *Lygus*.

General bud damage in alfalfa is illustrated in figure 1. For comparison, figure 2 shows racemes of healthy buds, flowers, and seed pods that are borne on long peduncles or stalks.

METHODS AND MATERIALS

The nature of *Lygus* damage to alfalfa buds was studied in artificially infested material, with the raceme or cluster of buds taken as a unit. Undamaged specimens were obtained for infestation by tying parchment bags over the tips of stems or branches from which previously formed buds and flowers had been removed, thus permitting the development of new buds in the complete absence of *Lygus*. Racemes of buds from one-eighth to three-eighths of an inch in length were enclosed in sets of four per bag for infestation with either one or two adult *Lygus*, or were exposed to the natural bug population of the seed fields. Check treatments were obtained by enclosing racemes of buds without infestation. The different treatments were applied to racemes of buds on the same plant, and they were repeated with a large number of racemes on several varieties and strains of alfalfa at different times during the seed-setting season. The period of infestation was varied from 20 to 48 hours, after which the insects were released and the bags were replaced to protect the buds from further damage through chance infestation. For evidence of damage based on color, condition, and general appearance, an examination of the racemes of buds was made on the fifth to seventh day after the initiation of the infestations.

A similar procedure was followed in an attempt to determine the effects of *Lygus* bugs on alfalfa flowers, except that the individual flower and not the raceme of flowers was taken as the unit. The flowers on approximately one-half of the racemes were tripped by hand, after which infestation was effected in the manner described for the buds.

Infested and uninfested buds and flowers were preserved in formalin acetic alcohol for histological study. Green and unpreserved material

was useful in a study and description of the general symptoms of damage. Further details of *Lygus* injury could be identified best from a microscopical examination of buds and flowers embedded and stained by ordinary methods. Microtome sections were cut 12μ thick and mounted in serial and chronological order to facilitate tracing the course and rate of spread of the cell disintegration origi-

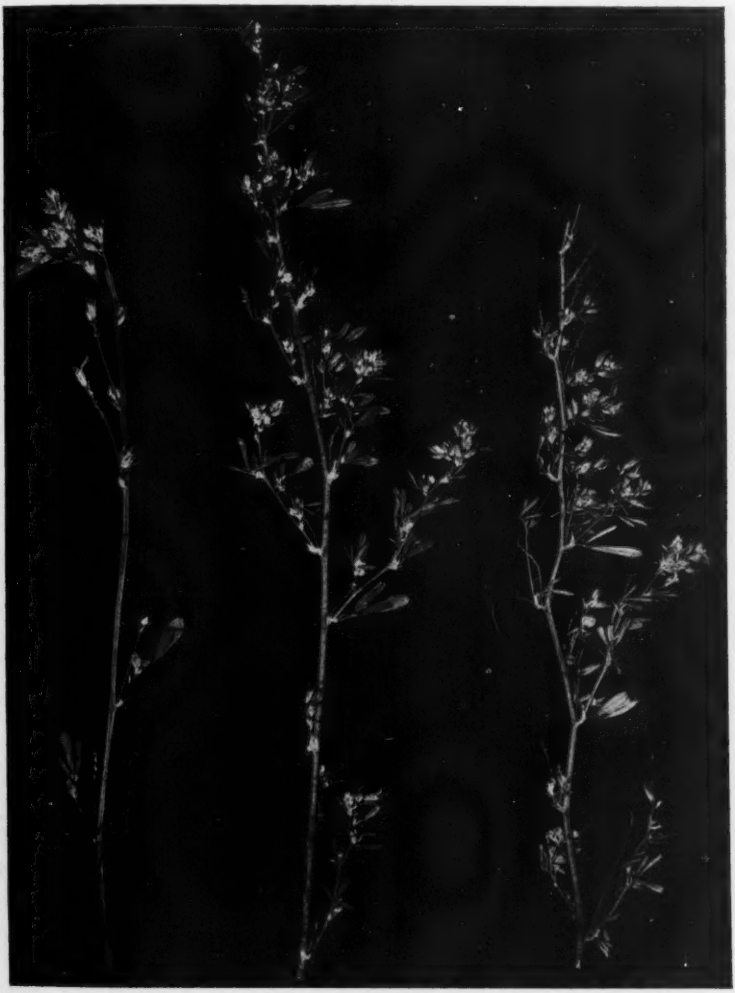

FIGURE 1.—Terminal portions of three alfalfa stems showing *Lygus* damage. The racemes of buds are small, unusually numerous, crowded, and generally discolored. A tendency to excessive branching and the development of short internodes near the stem terminals is shown. Specimens from an alfalfa field heavily infested with *Lygus* bugs. (Approximately one-half natural size.)

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nating from punctures. Various stains were used. The best results were obtained with Delafield's haematoxylin and with a combination of safranin with light green. Details of cell structure and embryo development were shown especially well with Heidenhain's iron-alum

FIGURE 2.—Terminal portions of three alfalfa stems showing an approximately normal development of buds, flowers, and seed pods. A normal elongation of the internodes and the occurrence of the racemes of buds and flowers on long peduncles are shown. Crowding of the inflorescences is not apparent and most of the racemes have a large number of buds and flowers, a large proportion of which develop into seed pods. Specimens from an isolated plant far from cultivated fields of alfalfa. (Approximately one-half natural size.)

haematoxylin. Generally unsatisfactory results followed a few attempts to trace the origin and course of the damage in buds and flowers without the embedding and staining technique.

NATURE AND EXTENT OF DAMAGE

The initial damage resulting from feeding punctures by *Lygus* is definitely localized. The extent of damage to young buds that may occur under different intensities of infestation is shown in table 1. A single puncture may be seen under the microscope as a small perforation surrounded by a collarlike area of discoloration. (See pl. 1 and fig. 6.) Superficial evidence of damage to buds is indicated by a slight bleaching that becomes apparent 24 to 48 hours after infestation. Death and complete disintegration of the injured buds may follow in a few days. Dead buds frequently remain attached to the floral axis and retain more or less the size and shape they had at the time of injury. Discoloration and disintegration of injured buds begin at the punctures and are apparently caused by a toxic or irritant substance that is emitted with the saliva of the insects at the time of feeding. This observation is supported by the work of Smith (*9*), who studied the feeding methods of capsid bugs (Miridae) which are closely related to *Lygus*. He showed by removing the salivary glands of harmful and harmless species and placing them on apple fruit and foliage and pricking slightly the cells beneath with a fine needle that the damage is chemical rather than physical in character. King and Cook (*7*) showed that *Lygus* bugs and closely related species feed by the same process, namely, by inserting their mouth parts into plant tissue and sucking the sap, but that more serious pathological effects follow feeding by some species and individuals than by others.

TABLE 1.—*Average percentage of racemes of buds apparently normal and of those apparently injured (after 20 to 48 hours' infestation with Lygus bugs* [1]

Infestation	Plants	Racemes	Racemes apparently in condition indicated	
			Normal	Injured
Number of *Lygus* to 4 racemes of buds	*Number*	*Number*	*Percent*	*Percent*
0	29	116	80.0	20.0
1	17	68	15.6	84.3
2	20	80	13.7	86.2
Natural (field)	25	100	25.0	75.0

[1] Condition of buds determined from evidence of damage based on color and appearance on the fifth to seventh days after infestation began.

The inception and development of *Lygus* damage in alfalfa buds was shown by infesting four normal racemes of buds with four bugs for a period of 12 hours. After the insects were released, the buds were again enclosed and left sufficiently long to allow for the development of different degrees of damage. One raceme of buds was fixed for histological study at the end of the 12-hour infestation period, while others were collected for preparation and study after periods of 24, 36, and 48 hours. In some trials the infestation period was increased by 12-hour intervals up to 60 hours, after which fixation of buds for histological study was made at 12-hour intervals. It was

EXPLANATORY LEGEND FOR PLATE 1

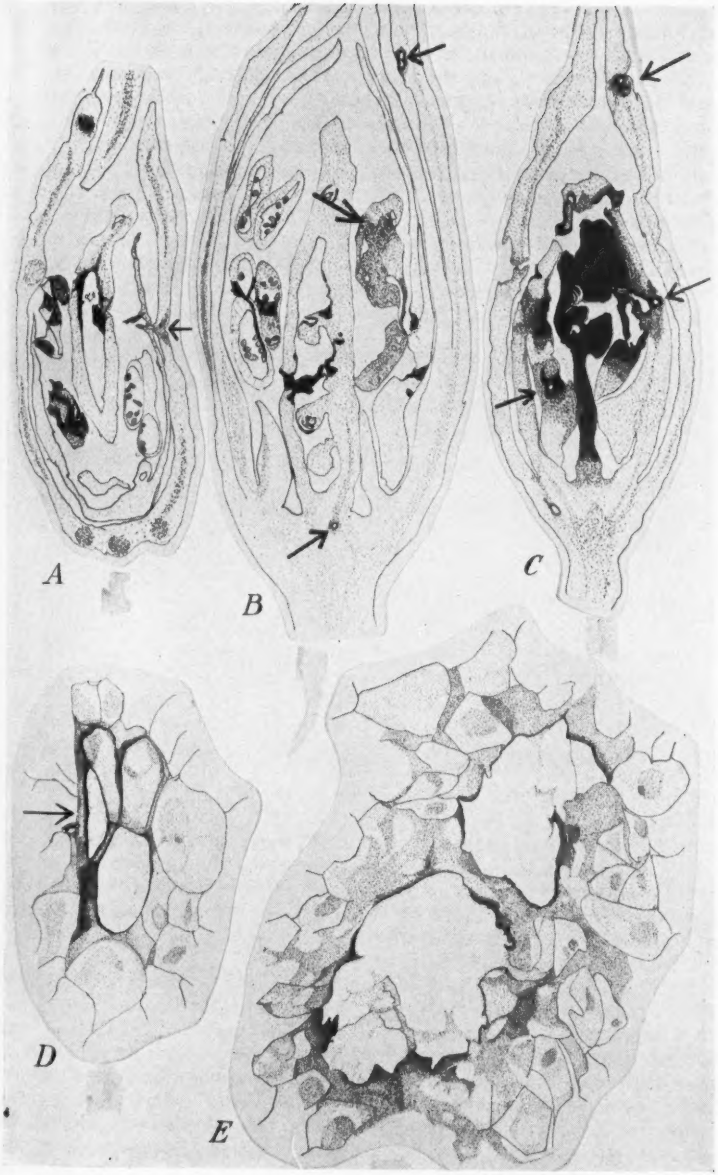
A, Longitudinal section through a young bud from a plant damaged under a natural infestation in the field. The course of a puncture through the floral envelope is shown; it extends into the ovary where an area of cell disintegration has been initiated. (Approximately 42 times natural size.)

B, Longitudinal section through an older bud that was artificially infested with *Lygus*. Localized areas of discoloration and disintegration are shown in which the evidence of punctures has been largely obliterated (*B*, *a*). Recently made punctures are shown near the basal portion of the ovary and in the floral envelope near the apex of the bud. A general disorganization of the bud has resulted. (Approximately 42 times natural size.)

C, Longitudinal section of a young bud that was infested for 48 hours. An advanced stage of disintegration is shown. Arrows point to punctures and centers at which disintegration began. (Approximately 42 times natural size.)

D, Small puncture made by an insertion of the proboscis and showing the early stages of cell discoloration and disintegration. (Approximately 42 times natural size.)

E, Two approximately 24-hour-old punctures showing a comparatively extensive area of disorganization and discoloration. (Approximately 740 times natural size.)



CAMERA LUCIDA DRAWINGS OF ALFALFA BUDS DAMAGED BY LYGUS.

FOR EXPLANATORY LEGEND SEE OPPOSITE PAGE.

difficult to trace the origin and course in the development of the damage after long infestation, or in material that had developed to advanced stages of deterioration. An infestation of from 12 to 24 hours, with a comparatively short period in which the deterioration might develop, gave evidence that the bud damage had in most cases been initiated from *Lygus* punctures. Extensive disintegration of buds appeared also to have resulted, apparently from the effects of the toxic substance injected into the plants by the insects.

A determination of the nature of *Lygus* damage in alfalfa cannot always be made from material infested in the field. Advanced stages of bud disintegration sometimes obliterate all evidence of the original punctures. Identification, however, can usually be successfully made from artificially infested racemes of buds when sectioned on the microtome, stained, and examined under the low power of the microscope. Numerous punctures made by repeated insertions of the proboscis of the insect have been found within a portion of a single bud. Areas of disintegration absorb the stain more readily than the undamaged parts of buds and can thereby be easily recognized. Mechanical damage resulting directly from *Lygus* feeding punctures is apparently of local and rather limited effect. It appears that major damage develops from secondary or indirect effects, such as distorted vegetative growth and profuse proliferation, which are discussed in detail in a later section of this paper. Recovery from the effects of an infestation of short duration is sometimes noticeable from 5 to 10 days after the application of an insecticide to remove the insects.

BUD ROSETTING

Especially distinctive symptoms of *Lygus* damage to alfalfa result from the development of racemes of buds near the tips of main stems and branches into disklike or knoblike structures called rosettes (fig. 3).

Bud rosetting has been shown to occur under heavy *Lygus* infestation, but this, apparently, is not the only cause of abnormal bud development. The condition is common in Utah alfalfa fields that are setting a poor crop of seed. The compressed state of the racemes of buds appears to result from a failure of the upper internodes of a stem or branch to elongate to the usual length, and from a differential growth in the individual racemes composing the cluster. Racemes of buds in a rosette are, as a rule, small, discolored, and tightly compressed. Frequently most of them fail to produce well-developed clusters of flowers that set seed pods, although considerable variation has been observed in this respect.

Bud rosetting developed in repeated trials on 8 or 10 seedling alfalfa plants from which all previously formed buds and flowers had been removed, when enclosed in cheesecloth cages and infested with 300 late-instar and adult *Lygus*. The rosetting became noticeable on the third day of the infestation when the original number of insects was doubled to increase the severity of the effects. The heavier infestation resulted in a condition that was typical also of field plants outside of the cages. A still further increase in the intensity of the infestation was made at the end of the fourth week by the addition of 150 *Lygus* to the survivors of the original number of bugs in each cage, which resulted in severe and continued damage to the buds for

the remainder of the season. Uninfested plants in check cages did not develop the rosetting, but produced an abundance of flowers from which only a few seeds pods were obtained, owing probably to the unfavorable effects of shading during the long period of enclosure and the failure of the flowers to become fertilized.

The exact nature of bud rosetting has not been determined. Microscopic examinations of rosettes produced under controlled infestation have shown punctures and a bud disintegration generally characteristic of *Lygus* damage. In addition, however, a disturbed growth and development in the stem terminal and bud primordia is apparent. Eggs of insects, which measurements have shown to correspond closely in size and form to those of *Lygus*, have frequently been found in rosettes and in the upper nodes of a stem. Large cavities are also sometimes made in the stem terminals during oviposition, and mechanical destruction of plant tissue may result in some degree. Comparatively little disintegration of cells has been noted surrounding egg cavities. It is possible, nevertheless, that extensive mechanical destruction of cells near the stem tips during oviposition may affect the normal development of structures initiated from the growing point and result as well in a suppressed elongation of terminal internodes.

FIGURE 3.—A suppressed elongation of the apical internodes of alfalfa stems and the development of racemes of buds in clusters called rosettes. The condition occurs under severe *Lygus* infestation. Compare with normal condition (fig. 2). (Approximately one-half natural size.)

BUD ABORTION

Damage to alfalfa described as bud abortion occurred in 20 percent of the racemes of buds from which *Lygus* was excluded in the controlled infestation experiments (table 1). Physiological conditions affecting growth and development of the buds, however, appear to be the principal causes contributing to this type of damage. Bud abortion is apparently not unusual, since it has been observed in greenhouse plants and was shown to develop in 21 of 29 field plants on which racemes of buds were enclosed for protection from *Lygus*.

Bud abortion in alfalfa is illustrated in figure 4. The important characteristics are the small size of the racemes of buds and the intense buff-colored bleaching that is conspicuous against the green of healthy stems and leaves. The microscopic character of the bud disintegration and break-down is shown in figure 5, in which it appears to occur uniformly and over the whole raceme at approximately the same time. Damage resulting from bud abortion is distinctly unlike that which develops from *Lygus* infestation. Bud abortion in alfalfa seed fields sometimes complicates the identification of *Lygus* damage, although the two types of damage appear distinctly unlike under microscopic examination.

FLOWER FALL

Flower fall in alfalfa may result from various causes of which insect damage is of great importance. *Lygus* injury to alfalfa flowers is

FIGURE 4.—Bud abortion in alfalfa; not caused by *Lygus* but due to conditions that are unfavorable to bud development and growth. (Approximately one-half natural size.)

shown in sectioned and stained material as punctures and lacerations in the ovaries similar to that occurring in young buds. Damaged individual flowers, however, abscise and are shed so soon after injury that discoloration or disintegration is not conspicuously noticeable while they remain attached to the plant. Excessive flower fall in alfalfa occurred under controlled *Lygus* infestation when either 3 or 5 bugs were enclosed with 7 to 10 flowers for 48 hours (table 2). The percentage of flowers falling was about the same with artificially tripped flowers as with those under natural development, although a higher percentage of the surviving tripped flowers set seed pods. Numerous observations have shown *Lygus* bugs to be an important cause of excessive flower fall in alfalfa seed fields, although these insects are by no means the only cause of low yields and poor seed crops.

Alfalfa is highly variable in its reproductive behavior and is sometimes known to shed its flowers in the apparent absence of destructive

insects. Brink and Cooper (*2*) have shown that the degree of effective pollination is very commonly a limiting factor for seed production. Cooper et al. (*6*) have demonstrated that a failure of seed setting in alfalfa where the flowers have been tripped to insure effective pollination is apparently due to lack of fertilization even though pollen tubes are present. The pollen tubes sometimes fail to reach all the ovules, and even when fertilization is effected, embryo abortion may occur at various stages in development. More recently Tysdal (*12*) has shown the importance of tripping insects, particularly wild bees of *Nomia* and *Megachile* species, as pollinators of alfalfa flowers, and he has shown that the presence of these insects in alfalfa seed fields is frequently correlated with satisfactory yields of seed.

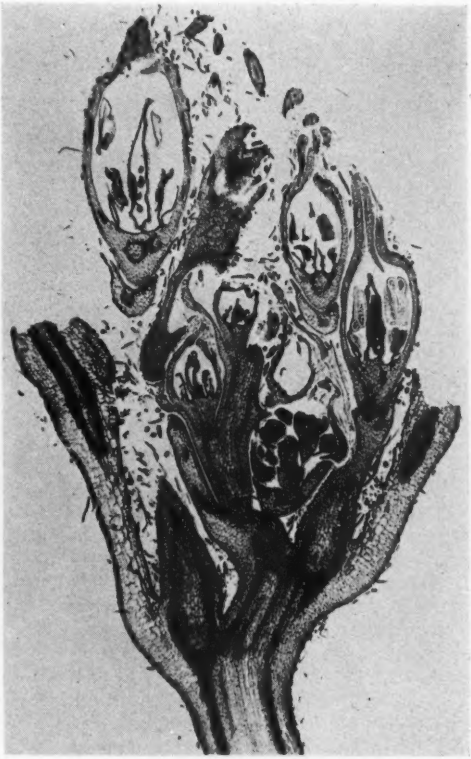


FIGURE 5.—Photomicrograph of median longitudinal section through a raceme of young aborted alfalfa buds. The break-down and disintegration of the individual buds is general and uniform over the whole raceme, in contrast to the localized disintegration that follows *Lygus* damage. (Approximately 25 times natural size.)

The nature of *Lygus* damage to alfalfa flowers is illustrated in figure 6. A puncture has been made through the floral envelope and into the lower extremity of the ovary. A collarlike area of discoloration surrounds the perforation. The originally small area of injury has become enlarged and has resulted in a partial disintegration of the lower one-third of the ovary. A generally extensive area of damage is shown within the ovary and appears to have destroyed about one-half of the ovules. Most of this damage appears to be traceable to the effects of a single puncture.

A condition of alfalfa flowers that fall from causes other than insect damage is illustrated in figure 7. A shriveling and deterioration of the ovules occurs without evidence of punctures, lacerations, or other mechanical injury, and with no indication of a deterioration due to toxic effects. The appearance of the ovules suggests a failure in development due to a lack of fertilization, or an embryo abortion

following fertilization that has resulted in the development of shriveled seeds.

TABLE 2.—*Average percentage of normally developed and of artificially tripped alfalfa flowers that fell while exposed to an infestation of Lygus bugs for 48 hours and average percentage of the total flowers that formed seed pods within 10 days after infestation period*

Infestation [1]	Plants	Flowers of indicated treatment falling during infestation period and those setting seed pods within 10 days after infestation [2]			
		Normal development		Artificial tripping	
		Flowers falling	Setting seed pods	Flowers falling	Setting seed pods
Number of *Lygus* per 7 to 10 flowers:	*Number*	*Percent*	*Percent*	*Percent*	*Percent*
0	40	9.3	10.3	5.8	52.2
1	15	32.1	4.4	32.1	26.5
2	15	36.0	4.2	30.4	9.0
3	5	80.8	2.1	64.6	20.8
5	5	97.9	0	89.1	.5
Natural (field)	40	6.9	22.5	9.4	38.6

[1] Adult *Lygus* enclosed with flowers in paper bags; released at the end of 48 hours, after which the bags were replaced over the flowers.
[2] Remainder of the flowers not forming seed pods fell after the infestation period.

SECONDARY EFFECTS OF LYGUS DAMAGE IN ALFALFA

METHODS AND MATERIALS

The pathological symptoms appearing in the buds and the damage suffered by alfalfa plants infested with *Lygus* bugs led to inquiry regarding possible physiological disturbances in growth and reproductive development that might impair the plants for seed setting. *Lygus* infestation and insecticide treatments were applied to transplanted, hill-spaced, alfalfa seedlings of Grimm, Hardistan, Kansas Common, and a heavy seed-producing strain of a Wisconsin Grimm selection. The plants of the different alfalfas were spaced 3 by 3 feet apart in random order and within partly isolated blocks a rod square. The special purpose of the isolation was to eliminate the drifting of the insecticide from treated to untreated plots during application.

Treatments were begun on June 20, when all plants were in the prebud stage of development and approximately 8 inches high. Infestation was effected by using cheesecloth cages to confine the *Lygus* bugs to the plants for a period of 24 hours. Once established, the infestation was maintained by adding to each plant, from time to time, the number of bugs necessary to produce a damage approximately as severe as that occurring naturally in nearby alfalfa fields. Prevention of damage by the insects on control blocks was effected by the frequent application of a dry pyrethrum concentrate containing 2 percent pyrethrins, in the proportion of 15 parts to 85 parts of colloidal or electric dusting sulfur as a carrier.

Variations in the rate or frequency of application of the insecticide were not made, since a maximum control of the insects and a prevention of the damage was all that was desired. Infestation and control treatments were applied to blocks in duplicate as follows:

Treatment 1.—Infested with *Lygus* bugs from the prebud stage to the full-bloom stage of development. Dusted after the full-bloom stage five to seven times weekly until seed harvest. Objective: To determine the effects of *Lygus* infestation during the early vegetative stages of growth and development of alfalfa, and the later effects on seed setting.

Treatment 2.—No infestation; dusted five to seven times weekly from the prebud stage of development of the plants to seed harvest. Objective: To determine the type of growth and development in alfalfa and the effects on seed setting when plants are comparatively free from *Lygus* infestation.

Treatment 3.—Same as for 2, except the early buds and flowers were clipped by hand to approximate the damage resulting from *Lygus* infestation under treatment

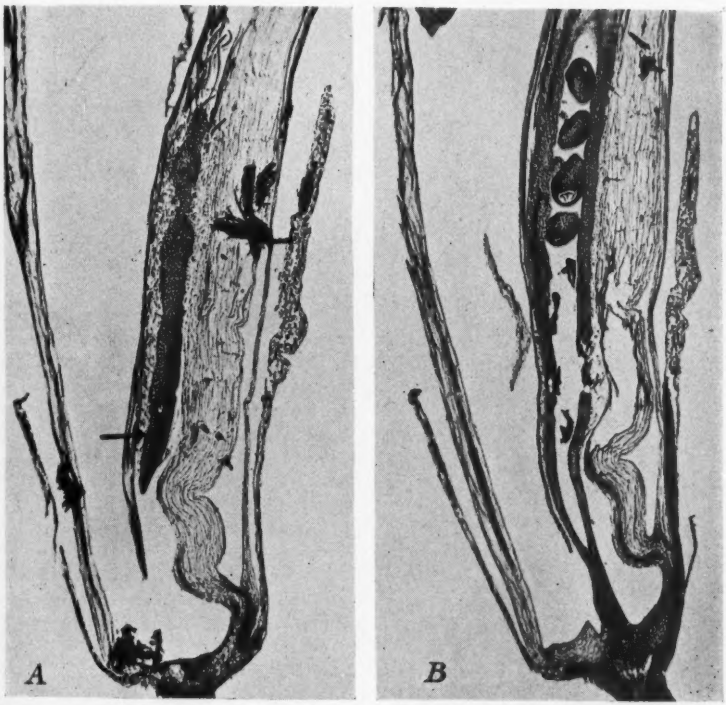


FIGURE 6.—Photomicrograph showing the effects of a *Lygus* puncture in the ovary of an alfalfa flower. *A*, Oblique longitudinal section exposing the ovary and showing a puncture that has resulted in a discoloration of the basal one-third of the ovary. *B*, Median longitudinal section from the same flower, exposing the ovules and the area of damage within the ovary. The localized nature of the damage is shown. The ovules in the upper one-half of the ovary are apparently free from injury.

1. Objective: To determine the effects on growth, development, and seed setting in alfalfa when the loss of buds and flowers occurs from causes other than *Lygus* damage.

Treatment 4.—Infested continuously with *Lygus* from the prebud stage of growth and development until seed harvest. Objective: To determine the effects of continuous *Lygus* infestation on alfalfa, with special reference to effects on seed setting.

Treatment 5.—Uninfested and dusted from the prebud stage to the full-bloom stage of development. Thereafter, infested with *Lygus* until seed harvest. Objective: To determine the effects of *Lygus* infestation during the bud and the flower stage of alfalfa development in relation to seed setting.

EFFECTS OF LYGUS INFESTATION ON EARLY GROWTH AND DEVELOPMENT OF ALFALFA

The average height of the plants in the various blocks previous to infestation ranged from 6.9 to 9.1 inches. Fifteen days after infestation the infested plants had an average height of 12.3 inches, as compared with an average height of 17.2 inches for uninfested plants that were dusted frequently. At the end of 22 days, when the plants were in full bloom, the average heights were 14.5 and 21.3 inches for infested and dusted plants, respectively. The effects of the two treatments on growth of the plants are illustrated in figure 8. The photographs were taken to the same scale to show these effects directly.

FIGURE 7.—Photomicrograph of a median longitudinal section of an alfalfa flower that has fallen from a raceme from a cause not directly attributable to *Lygus* injury. A shriveling and deterioration of the ovules is shown, with no apparent damage to the floral envelope or the ovary. The condition is typical of a large percentage of dehiscing alfalfa flowers and may result from failure of pollination, lack of fertilization, or embryo abortion.

Infested and dusted plants, with the exception of those in one block, developed approximately the same number of main stems (table 3). An average of 40.8 branches developed on 3 main stems of infested plants, as compared with an average of 25.5 on the uninfested and dusted plants. Wide variations in the tendency to profuse branching was shown by plants within blocks receiving the same treatment. Differences in response to infestation shown by the plants are probably due, at least in part, to a difference in the intensity or duration of the infestation occurring with individual plants within the same block. Excessive branching, which gives to affected plants an appearance of "stringiness," seems to result from a stimulation into activity of normally dormant axillary branch primordia due to *Lygus* injury at apical growing points of main stems and branches. Infested and uninfested plants developed approximately the same number of leaves on 3 main stems. The appearance and condition of the leaves, however, was strikingly different. An average of 21.8 percent of leaves from infested plants were crinkled or misshaped, as compared with 1.6 percent of those from the dusted

plants. Attempts to produce the leaf deformity by exposing young leaves to direct attack by the insects did not give rise to characteristic symptoms. It is possible that injury may occur indirectly to leaf-bud primordia and this results later in the development of crinkled and deformed leaves. An objection to this view arises from the fact that *Lygus* damage to young flower buds, which are probably less sensitive

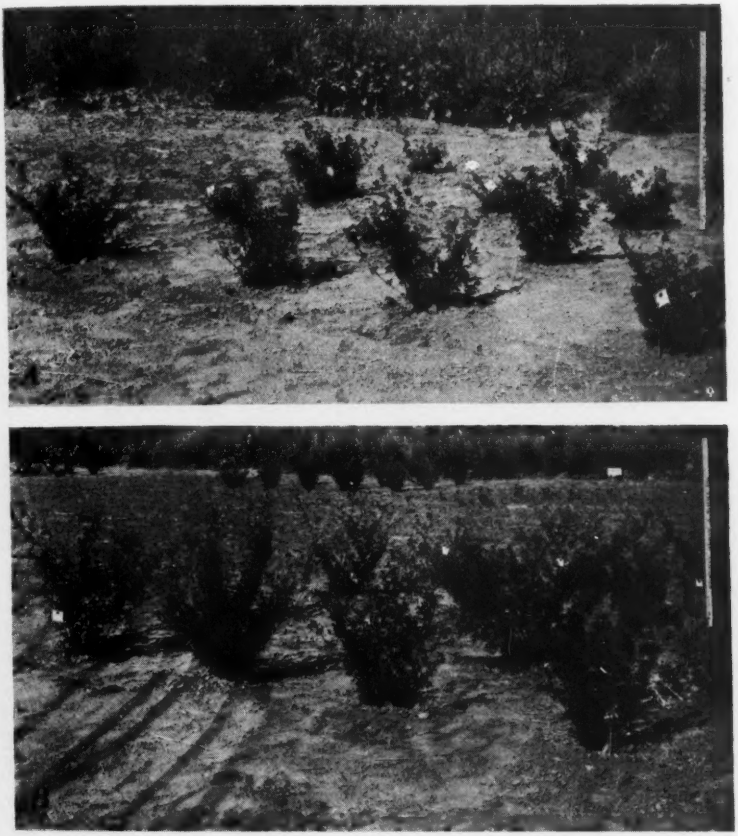


FIGURE 8.—Effects of *Lygus* infestation on the early growth and development of alfalfa plants: *A*, Infested from prebud stage to full-bloom stage of development; *B*, Uninfested and dusted five to seven times weekly for the same period.

to injury than leaf-bud primordia, results in immediate and complete deterioration. Nevertheless the variability in the number and proportion of crinkled and deformed leaves on plants within the same block and on different blocks and the tendency to profuse branching, as well as crinkled leaves, suggest *Lygus* as a direct cause.

TABLE 3.—*Comparative growth and development of alfalfa when infested at the prebud stage of development with Lygus bugs and when uninfested and dusted 5 to 7 times weekly with an insecticide*

Treatment	Growth and development of alfalfa [1]						
	Average height			After 15 days' treatment			
	Before treatment	After 15 days	After 22 days	Average stem per plant	Average branches per stem [2]	Average leaves per stem [1]	Crinkled leaves
	Inches	*Inches*	*Inches*	*Number*	*Number*	*Number*	*Percent*
Infested with *Lygus:*							
Block A	7.1	11.3	14.0	13.1	34.1	79	32.9
Block B	9.0	13.3	15.0	13.6	47.6	121	10.7
Mean	8.0	12.3	14.5	13.3	40.8	100	21.8
Dusted 5 to 7 times weekly:							
Buds not clipped:							
Block A	7.5	15.7	21.4	13.0	20.8	101	1.9
Block B	9.1	19.0	22.8	12.8	27.8	108	.9
Mean	8.3	17.3	22.1	12.9	24.3	104	1.4
Buds clipped:							
Block A	6.9	16.1	19.6	13.0	21.3	102	2.9
Block B	8.8	18.1	22.0	9.8	32.3	120	.8
Mean	7.8	17.1	20.8	11.4	26.8	111	1.8

[1] 16 plants per block. [2] 3 main stems.

DEVELOPMENT OF PLANTS FOLLOWING REMOVAL OF LYGUS

The *Lygus* bugs were removed effectively from infested blocks after repeated and frequent application of the insecticide. Evidence of a general recovery from the effects of a relatively brief infestation also became noticeable 10 days after the removal of the insects. Growth occurring subsequent to removal of the insects gave an appearance of having been superimposed on the previously damaged stems and branches. The first buds and flowers to develop after the removal of the insects appeared on short branches, as shown in figure 9. Later, longer stems and branches developed which had internodes of the usual length and buds and flowers borne on long peduncles, as is characteristic of normal and healthy alfalfa (figs. 10 and 2).

No marked effects resulted from clipping of the early formed buds and flowers under treatment 3. Neither were harmful effects observed to follow the use of the insecticide, at this stage of the investigation. Growth and floral development of frequently dusted plants were thought to be generally good and were apparently normal in all respects. Buds and flowers were produced in the abundance and succession characteristic of alfalfa growing under favorable conditions. Later it was observed that applications of insecticides having sulfur as a carrier resulted in a slight burning of the flowers, which damage has since been shown to result in reduced yields of seed.

EFFECT OF LYGUS INFESTATION IN THE FULL-BLOOM STAGE OF ALFALFA

Lygus infestation initiated in the full-bloom stage of alfalfa resulted in damage to buds and flowers and a condition similar to that commonly observed in commercial seed fields when producing a poor crop of seed. Discolored buds and an excessive flower fall gave early evidence of damage, while rosetting developed as a later effect.

Microscopic examination of injured buds showed characteristic *Lygus* punctures similar to those obtained under more closely controlled infestation. Growth and development of the plants were not retarded by late infestation. The usual "stringiness," however, gave to the plants an appearance of excessive vegetative development. In general flowers were produced abundantly, although most of them

FIGURE 9.—Stem from a *Lygus*-infested alfalfa plant showing distorted development and a tendency to excessive branching. Racemes of buds, flowers, and seed pods that are apparently normal (fig. 2) developed on short branches soon after the removal of the infestation by frequent dusting.

abscised early and before seed pods were formed. The production of seed was also generally poor.

EFFECTS OF LYGUS INFESTATION ON SEED AND FORAGE PRODUCTION

Seed yields from plants receiving different infestation and insecticide treatments differed strikingly (table 4). The highest yields of seed per plant resulted from uninfested plants that were dusted frequently

to control *Lygus*, while the lowest yields were obtained from those undusted and continuously infested. Differences in the yield of seed resulted also from variations in the time of applying the infestations to plants in different stages of vegetative and reproductive development. Generally good agreement in yields is shown by replicates of the various treatments, which is evidence of a satisfactory control of *Lygus* under the conditions of the experiment.

FIGURE 10.—Type of growth and reproductive development on severely damaged alfalfa plants following the removal of a *Lygus* infestation. Below the line: Retarded and distorted stem development and excessive branching that is typical of the effects of *Lygus* on early growth and development of alfalfa, except two branches at the extreme right. Above the line: Growth and development that followed the removal of the infestation. Note the normal elongation of the stem internodes and the development of racemes of buds and flowers on long peduncles, as is the normal condition in alfalfa (fig. 2).

Mean yields of slightly more than 12 gm. of seed per plant, which were obtained from the uninfested and dusted plants, are estimated to be equivalent to an acre yield of from 200 to 300 pounds. This estimate is based on the yields of many 1-year-old hill-spaced alfalfa plants at the Uinta Basin Alfalfa Seed Experimental Farm of the Utah Agricultural Experiment Station in years when successful seed crops were produced. The approximation is subject to some error owing to differences in the degree to which young hill-spaced alfalfa plants utilize effectively and efficiently the space allotted to each, but is, nevertheless, of value as a means of providing some idea of the beneficial effects that might be expected from a control of *Lygus*. The low average yield of 2.30 gm. of seed per plant obtained from the plots infested with *Lygus* would not, on the same basis of comparison, be expected to pay for the costs of harvesting and threshing.

The differences in yield of seed shown by infested and insecticide-treated plants are highly significant statistically. Differences resulting from varying the time of the infestation in relation to stages in the development of the plants are small but near the border line of low statistical significance. The consistently low yields of seed obtained under continuous *Lygus* infestation are evidence that greater damage to seed production results from long and continued *Lygus* infestation than from short or

periodic infestations of limited duration. More serious damage to seed production seems to have resulted from *Lygus* infestation in the full-bloom stage than from infestation in the early stages of vegetative development. Infestation at any time, however, may be expected to result in some damage. Clipping the early buds and flowers of uninfested and dusted plants, as in treatment 3, produced no statistically significant effect on seed production as compared with treatment 2, in which they were allowed to grow and to which the same insecticidal treatment was applied.

TABLE 4.—*Average yield of seed in grams per plant of 16 alfalfa plants (per block) spaced uniformly in square rod blocks when infested with Lygus bugs at various stages of growth and development and when uninfested and dusted 5 to 7 times weekly with an insecticide*

Treatment of alfalfa plants [1]	Yield and quality of seed			
	Average seed per plant			Average proportion of good seed
	Block A	Block B	Mean	
	Grams	*Grams*	*Grams*	*Percent*
1. Infested during the prebud stage and dusted in later bloom stages	5.80	8.35	7.07	75.8
2. No infestation; frequent dusting	11.85	10.13	10.99	83.0
3. Same as 2 (early buds clipped)	12.51	14.85	13.68	80.2
4. Continuous infestation	3.15	1.46	2.30	48.6
5. Dusted during the prebud stage and infested in bloom stage	2.91	4.25	3.58	63.9
Significant difference (5-percent point)			3.59	18.5

[1] For complete description of treatments, see p. 803.

Significant differences were obtained in the quality of the seed produced under continuous *Lygus* infestation and that produced under frequent insecticide treatment (table 4, last column). *Lygus* is, therefore, shown to affect the quality and value of alfalfa seed, as well as to damage buds and flowers. A high shrinkage in recleaning, which in some cases exceeded 50 percent, has occurred in commercially produced crops in years when *Lygus* has been suspected as a cause of the low yields.

The average weights of air-dry forage produced by the alfalfa plants under different infestation and insecticide treatments are given in table 5. Generally good agreement in some cases and wide differences in others are shown between the mean weights of the plants in the two replicates of the treatments. A statistically significant difference is shown between the mean weight of the plants under continuous *Lygus* infestation and that of the plants in the other treatments. The data are probably insufficient to permit definite conclusions as to the effects of *Lygus* on the vegetative development of alfalfa. General experience and observation in the production of alfalfa seed under *Lygus* infestation have shown that on good soil and with a not too restricted water supply, vegetative growth sometimes becomes excessive to the extent that cutting and threshing of poor seed crops becomes difficult and costly. It is not known definitely, however, whether this excess growth results from a failure of the plants to set seed or from a stimulation due to *Lygus* injury (fig. 11).

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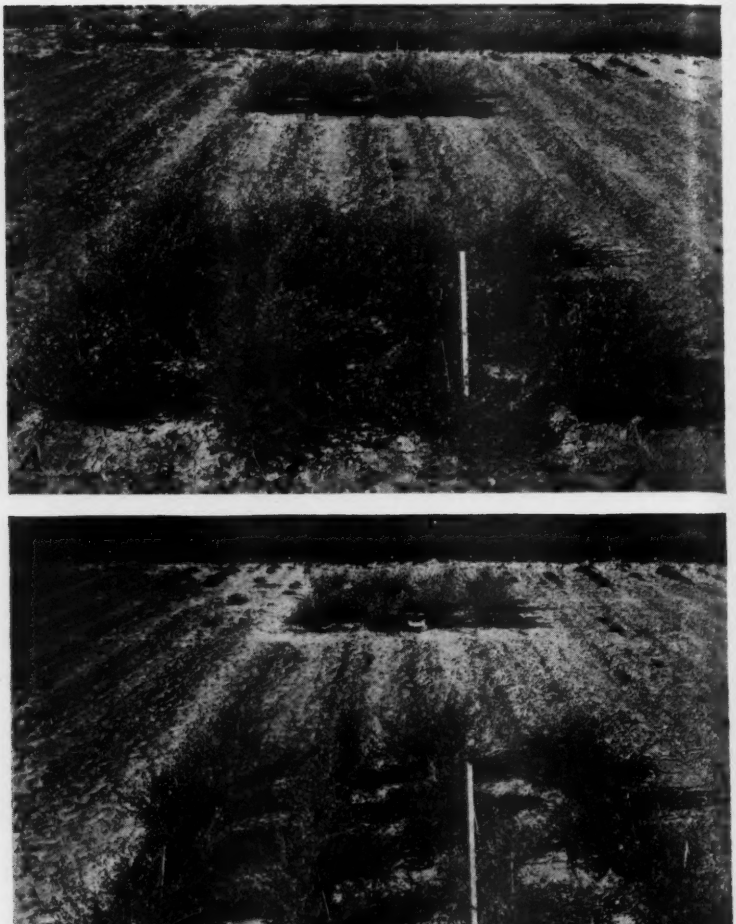

FIGURE 11.—Comparative growth and vegetative development of *Lygus*-infested and uninfested alfalfa plants: *A*, Continuously infested from prebud stage of development to seed harvest (treatment 4); *B*, uninfested and dusted five to seven times weekly for same period (early buds and flowers clipped; treatment 3). Photographs taken to the same scale. Compare the ground covered by the plants for an idea as to their relative size.

TABLE 5.—*Average weight of air-dry forage in grams per plant of 16 alfalfa plants spaced uniformly in square rod blocks when infested at various stages of growth and development with Lygus bugs and when dusted 5 to 7 times weekly with an insecticide*

Treatment of alfalfa plants [1]	Yield of air-dry forage		
	Average weight of air-dry forage per plant		
	Block A	Block B	Mean
	Grams	*Grams*	*Grams*
1. Infested during the prebud stage and dusted in late bloom stage	215	217	216
2. No infestation; frequent dusting	192	214	203
3. Same as 2 (early buds clipped)	204	209	206
4. Continuous infestation	254	259	256
5. Dusted during the prebud stage and infested in bloom stage	207	237	222
Significant difference (5-percent point)			29

[1] For complete description of treatments, see p. 803.

DISCUSSION AND CONCLUSIONS

It is in recent years only that attention has been given to *Lygus* bugs as pests in alfalfa seed production. While these insects are known to be widely distributed and to feed on a variety of native and cultivated host plants, comparatively little is known of their occurrence in alfalfa seed fields prior to the general onset of alfalfa seed crop failures in Utah. However, evidence gained from a study of the biology, life history, and general habits of *Lygus* in relation to alfalfa seed production (*10*); their occurrence and the intensity of the infestations in relation to alfalfa seed setting (*11*); and the nature of the damage, as determined in the present investigation, leaves little doubt as to the great importance of *Lygus* as a factor in alfalfa seed production at the present time. Since the *Lygus* species damaging alfalfa are native to western America, it is highly probable that they have been present in the alfalfa seed fields of the Western States for many years. It is not clear, however, as to how, when, and why they have apparently only recently become sufficiently numerous to constitute a pest of prime importance.

Brues (*3*) has shown that insects sometimes change their food habits and are known to leave their wild host plants and adopt new food plants among cultivated crops. Two weeds of the family Chenopodiaceae that are known to harbor *Lygus* in large numbers have become widely distributed in Utah alfalfa seed-producing areas since the land was first brought into cultivation. The best known and most widely distributed is Russian thistle (*Salsola pestifer* A. Nels.) and the other is smother weed (*Bassia hyssopifolia* (Parl.) Kuntze). *Chenopodium* species were early reported by McGregor (*8*) as the most common of the native host plants of *Lygus elisus* in the Imperial Valley of California. Winslow et al.[4] reported declining yields of alfalfa seed as beginning with the advent of sugar-beet seed growing in the Hemet Valley of California, which is significant in view of the fact that *Lygus* is also recognized as a pest of sugar-beet

[4] WINSLOW, E. M., HUBERTY, MARTIN R., and STITT, LOYD L. PROGRESS REPORT SURVEY OF ALFALFA SEED, HEMET VALLEY. Agr. Ext. Serv., Riverside, Calif. 8 pp. 1938. [Mimeographed.]

seed production in Utah by workers in the Division of Sugar Plant Investigations of the Bureau of Plant Industry, United States Department of Agriculture. Furthermore, somewhat limited experience by the Division of Forage Crops and Diseases in growing seed of improved strains of alfalfa in Utah has shown severe *Lygus* infestation and damage to develop on blocks adjacent to sugar beets. Less damage has been observed on blocks adjoining grassland, winter wheat, and fallow. Various conditions and complex ecological relationships may, therefore, be given consideration in an attempt to explain why *Lygus* has reached its present status as a major pest in alfalfa seed production.

Complete information is lacking also as to the conditions under which marked declines in yield of alfalfa seed have occurred. Certain striking similarities may be noted in the general sequence of events that have led to low yields of alfalfa seed in several widely separated regions. Production began in western regions, as a rule, on virgin soil and with a comparatively small acreage. The yields in the early years of production were often high, ranging from 400 to 1,000 pounds or more of seed to the acre. A peak in total production resulted, followed by declining yields and a low total production. While new lands were available, seed-producing areas were developed rapidly in new regions and seed growers continued production with profit for many years in succession. At the present time, certain of these same regions are characterized by frequent seed-crop failures, low acre yields, and generally low total production of alfalfa seed.

A few acres of alfalfa were planted on virgin land in the bottoms of Wah Wah Valley on the western desert of Utah in the summer of 1936. The severe bud damage and flower fall that are typical of *Lygus* injury were observed in the area the following year. Sweepings with an insect net showed the *Lygus* population to be as high as that in representative fields in the older alfalfa seed-producing regions of Utah and Idaho. The observation is of special interest because of the fact that the planting of alfalfa was the first to be made in the region and no other alfalfa fields were known within a radius of approximately 30 miles. The infestation had evidently developed through migration of *Lygus* from the native host plants of the desert. On the other hand, some outstandingly successful seed crops have been reported from fields bordering on the desert during a period of seed-crop failures in older seed-producing areas in Utah.

Carlson and Stewart (*5*) and Carlson (*4*) reported yields of alfalfa seed from experimental trials that ranged from less than 50 to more than 800 pounds of seed to the acre, depending upon treatments, varieties, soils, and seasons. The observed symptoms of damage to the buds and the excessive flower fall associated with some of the low yields seem to afford unmistakable evidence that *Lygus* damage, as it is now known, was present in the fields, and the insects were probably an important cause of the poor seed setting. Plots that produced maximum yields in one year frequently gave exceptionally low yields the following year and vice versa. Wide variations in yields occurred among plots receiving similar treatments in the same year and in different years. It has been shown (table 4) that severe *Lygus* infestation in the full-bloom stage of alfalfa resulted in greater damage to the seed crop than did infestation in earlier vegetative stages of

plant development. Yield fluctuations among plots receiving the same cultural treatment are, therefore, at least in part, probably explainable on the basis of differences in the severity and time of occurrence of *Lygus* infestations in the various plots.

Fluctuations in yield of alfalfa seed in commercial fields are frequently as great as those reported for experimental plots and seem to be attributable to the same general causes. Yields of alfalfa seed reported to exceed 800 pounds to the acre were being produced on scattered and isolated ranches on the western desert of Utah only 90 miles distant from the areas of outstanding seed-crop failures in Millard County in 1934. Generally high acre yields of seed and high total production were obtained in northern Utah and southern Idaho for several years when seed-crop failures occurred in the formerly highly productive areas of Millard County and the Uinta Basin of Utah. More recently, a decline in production has been noted in certain regions of northern Utah and southern Idaho, while a marked improvement in conditions favoring seed setting in alfalfa has become apparent in portions of Millard County. These wide fluctuations in seed yields within relatively small geographical areas seem to offer unmistakable evidence of the effects of local factors rather than general climatic changes. In addition, symptoms of damage attributable to *Lygus* and the presence of the insects in seed fields at critical periods in the development of the seed crops are strong evidence that these bugs are in some way responsible for the low yields of seed, especially when conditions are otherwise apparently favorable for seed production.

CONTROL OF LYGUS

Sorenson (*10*) reported that the application of insecticides for the control of *Lygus* on a large scale is insufficiently effective to justify the cost and that the bugs possess a high natural resistance to most insecticides now available. However, in the present investigation, the frequent application of pyrethrum concentrate and sulfur to small plots resulted in considerable improvement in seed production, but particularly in the condition of the buds and flowers previous to pod setting. The average yields of seed per plant on 10 seed-increase plots that were dusted frequently during the growth of the seed crop in 1938 were approximately 10 times those from similar plots in 1937 when the insecticide was not applied until after severe bud damage and flower fall had occurred. The improved yields resulting from the use of the insecticide in 1938 are especially significant in view of the fact that the alfalfa seed crop of that year from the commercial fields in the region in which the trials were conducted was one of the poorest on record.

Increased yields of alfalfa seed have resulted in some cases from various cultivation and sanitation practices attempted by commercial seed growers. Some of these methods have not been tested under experimental control in Utah, and recommendations cannot, therefore, be made at this time. In one case, a *Lygus*-infested alfalfa field in which dry grass was burned following the removal of the first hay crop showed a striking improvement in the appearance and condition of the buds and flowers on the subsequent growth of the alfalfa. The seed produced after the burning was reported to have exceeded 200 pounds

to the acre and was the best that had been produced in the field for several years. It was obvious from inspection that this seed crop was superior to those in adjoining unburned fields. Owing to prolonged drought during the spring of the following year, the grass was too scanty to make burning an effective method of destroying the insects in the field, and it was not therefore attempted by the seed grower. The hay, however, was cut at the usual time, and the treatment of the field was the same as in the previous year except for the burning of the grass. The effect was that the alfalfa became heavily infested with *Lygus*, severe damage was caused to the buds and flowers, and a generally distorted development of the plants was in evidence. The seed crop was generally poor and was reported as not exceeding 100 pounds to the acre.

SUMMARY

An investigation was made to determine the effects of *Lygus* bugs (*Lygus hesperus* Knight and *L. elisus* Van Duzee) on alfalfa (*Medicago sativa* L.) in relation to seed setting, and to gain evidence of the extent to which these insects have been a factor contributing to a rapid decline in alfalfa seed production in several formerly highly productive seed-growing regions of the Western States.

Several types of bud damage are found in alfalfa. A mechanical localized damage has been shown by controlled infestation to result directly from punctures and lacerations made by the mouth parts of feeding *Lygus* bugs, although pathological effects develop indirectly from the initial damage caused by the insects. Damaged buds show discoloration and evidence of deterioration in from 24 to 48 hours after injury. A rapid disintegration of the buds that apparently results from a toxic substance emitted with the saliva of the feeding insects follows injury.

Rosetting has been shown to occur under heavy *Lygus* infestation and is characterized by the development of racemes of buds near the tips of main stems and branches into disklike or knoblike clusters.

Bud abortion, another type of damage occurring in alfalfa, is apparently not attributable to *Lygus* infestation, but rather to physiological factors and conditions unfavorable to bud growth and development.

Individual alfalfa flowers abscise and are shed soon after injury by *Lygus*. Damage to flowers results mainly from punctures in the ovary or other succulent parts. However, all flower fall in alfalfa is not attributable to insect damage, but may be due also to factors affecting fertilization and embryo development.

Lygus injury apparently also affects the vegetative growth and development of alfalfa. Young growth when heavily infested is definitely retarded, and shows a tendency to excessive branching. A high proportion of the leaves of heavily infested plants may be crinkled or deformed.

Changes in the character of vegetative growth and reproductive development of alfalfa plants follow removal of a *Lygus* infestation. Evidence of recovery from damage usually becomes noticeable within 10 days.

Bleached and discolored buds give early indications of *Lygus* damage to alfalfa infested in the full-bloom stage of development. Rosetting

develops as a later effect. Vegetative growth of alfalfa is not retarded by late infestation, but severe damage to the buds and flowers may result.

Uninfested plants that received frequent applications of an insecticide gave significantly higher yields of seed than did infested plants. Infested plants, however, gave a significantly higher yield of air-dry forage, but it is not known whether the increased yield of forage resulted from the effects of *Lygus* injury or from a failure of the plants to set an abundance of seed. Numerous observations made during survey studies to determine the cause of alfalfa seed-crop failures have shown serious damage to alfalfa to result more or less directly in proportion to the *Lygus* population of the seed fields. *Lygus* bugs are, therefore, regarded as an important cause of the major alfalfa seed-crop failures in Utah.

The importance of *Lygus* as a factor affecting alfalfa seed production in Utah is evident also from the nature of the damage to the buds and flowers, and by the significant improvement in the yield of seed that is consistently obtained when *Lygus* bugs are effectively controlled.

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TOXIC EFFECT ON GERMINATING SUGAR-BEET SEED OF WATER-SOLUBLE SUBSTANCES IN THE SEED BALL[1]

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INTRODUCTION

Differences among sugar-beet varieties in the rate of seedling emergence are commonly observed. These varietal differences are generally more pronounced under laboratory conditions than in the field and may be apparent for a long or short period of time, depending upon the varieties under observation.

Results [2] obtained by C. H. Smith, of the United States Sugar Plant Field Laboratory at Salt Lake City, Utah, had shown that washing the seed balls in water prior to planting accelerated germination and that water alone was as effective as any of an extensive series of salt solutions at various concentrations. These results are in line with the findings of Stehlík and Neuwirth (*18*),[3] who concluded that a preliminary soaking in water was equal to any other seed treatment to which stimulative action had been attributed. No suggestion was made as to what was accomplished by washing or presoaking of seed. The rather inconclusive and contradictory findings on the debated issue of seed stimulation are reviewed by these authors, who challenge the evidence on seed stimulation.

The presence of substances in the seed or seed coat of several seeds that either inhibit or stimulate germinating seeds has been reported. Axentjev (*1*) reported that the inhibiting action of seed extracts is not dependent upon fluorescence, and that seed extract of *Phacelia* may inhibit germination before it is exposed to light. He stated that the action of *Phacelia* seed extract was not specific but that it inhibited the germination of some seeds and stimulated others. Mosheov (*12*), in reporting his work relative to the presence of germination-inhibiting substances in wheat, stated that the substances are not heat stable and that the inhibiting effect is greater in light. Lehmann (*10*) reported the presence of heat-labile, germination-inhibiting substances in the hulls of buckwheat seeds.

Juices from fleshy fruits have long been known to retard or inhibit the germination of seeds. Oppenheimer (*13*, *14*) first postulated the presence of specific inhibitors in fruit juices in addition to the osmotic effect. He was later supported in his conclusions by Fukaki (*5*), Reinhard (*15*), and Köckemann (*8*). Lavialle (*9*) and Litvinov (*11*) claimed that the inhibitory action was almost entirely due to the osmotic pressure of the fruit juices.

The germination of sugar-beet seed may be influenced by several factors, such as vigor of the embryo, seed-ball structure, and the environmental factors imposed. That substances may be present in the seed ball that either hasten or retard germination seems not to

[1] Received for publication September 3, 1940.
[2] Unpublished.
[3] Italic numbers in parentheses refer to Literature Cited, p. 829.

have been heretofore considered. The experiments herein reported relate to the toxic effect on germinating sugar-beet seed of water-soluble substances in the dried fruit of the sugar beet, and the relationship of these effects to laboratory procedure in germination tests.

MATERIALS AND METHODS

Four sugar-beet varieties developed in the curly top-resistance breeding program, Nos. 5194, 550, 523, and 68, were used in these studies. According to the experience at the Salt Lake City laboratory, variety 5194 germinates extremely rapidly, whereas variety 68 germinates so slowly that it has been a rather common practice to plant it a week in advance of some other varieties when relatively uniform emergence from the soil was desired. The other two varieties are intermediate in germination rate.

In commercial usage, the term "sugar-beet seed" refers to the glomerules made up of the matured flowers of the beet. The glomerule, or seed ball, may contain from one to several true seeds. In these experiments, comparisons of rate and total germination were made with seed balls and the naked seeds freed from the surrounding envelope. The naked seeds were obtained readily in quantity by grinding the seed balls in a hand coffee mill set to grind coarsely. Uninjured seeds freed from all pericarp tissue were picked out from the broken seed balls. For convenience, in this paper the term "pericarp" is used to designate all parts of the seed ball that are not seeds and includes the ripened ovary wall and closely related parts, such as the base of the perianth and the receptacle.

Two points of procedure proved to be rather crucial in the proper evaluation of factors influencing the germination of sugar-beet seed. By the use of both seed balls and naked seed it was possible to compare the germination of the true seed in connection with and independent of its pericarp. The use of a thin cotton substratum in Petri dish germinators prevented the leaching of water-soluble substances from the pericarp and also made it possible to see the seeds at all times. On several occasions striking differences were observed in the condition and rate of growth of sprouts, which indicated further damage than that shown by the number of seeds that failed to germinate.

Water-soluble substances from intact seed balls and from pericarp tissue were similar in their effect on the germination of naked seeds. The extracts were obtained by soaking seed balls at room temperature for 20 hours in five times their weight of distilled water, and filtering the liquid through filter paper. The cotton substratum in the Petri dishes was then moistened with 9 cc. of the filtrate, after which 50 naked seeds of variety 68 were placed in each dish. The lids were then replaced and the dishes held in the dark at approximately 24° C. The decrease in rate and total germination of naked seeds in the Petri dish when water extracts from seed balls were used, as compared with results obtained when distilled water was used, was taken as the measure of the toxic effect of each extract. Throughout the tests of extracts, naked seeds of variety 68 were used because they were uniform and easier to obtain. Repeated tests had shown that naked seeds of other varieties gave entirely similar responses.

From two to four replicates were used for each variety or treatment and the data were analyzed by Fisher's variance method (*3*). An analysis was made on the data obtained at each germination count

and also on the combined data, including all hours of count for each experiment. This made it possible to measure the varietal or treatment differences in both rate and total germination. In any single experiment there was not a significant difference between the errors for the separate hours of count. In view of this, the general error derived from the combined analysis of all periods of count was used. The data for each hour of count are taken from the same Petri dishes, so the analysis is very similar to a main and subplot arrangement (*4*).

The analysis of the data in table 2, for example, was keyed out as shown in table 1.

TABLE 1.—*Analysis of variance of germination of intact seed balls of four varieties of sugar beets including three periods of count*

Source of variation	Degrees of freedom	Mean square	Calculated *F* value	Significant *F* values	
				5 percent	1 percent
Between replicates	3	50.11	1.17		
Between varieties	3	7,229.00	168.58	3.86	6.99
Varieties × replicates (error—a)	9	42.88			
Between hours of count	2	725.39	52.87	3.40	5.61
Varieties × hours of count	6	5,854.50	426.71	2.51	3.67
Remainder (error—b)	24	13.72			
Total	47				

EXPERIMENTAL WORK AND RESULTS

GERMINATION RATE OF SEED BALLS AND NAKED SEEDS

There was a marked difference among the four varieties in rate and total germination when the germination of seed balls (containing 1 to several true seeds) was used as the basis for comparison (table 2). In 42 hours after the seed balls were placed to germinate, variety 68 had germinated 4 percent, while variety 5194 had germinated 88 percent. This varietal difference was not due to lack of viable seed in the seed balls of variety 68, for when the seed balls were cracked open it was found that 90 to 92 percent of them contained matured seeds. Furthermore, during preliminary seed treatments it had been found that, after thorough washing in water, from 88 to 92 percent of the seed balls of variety 68 would germinate in 192 hours.

TABLE 2.—*Comparative relationship of the rate and total germination of seed balls and naked seeds of four varieties of sugar beets*

Variety No.	Germination of seed balls after—			Germination of naked seed after—		
	42 hours	90 hours	192 hours	19 hours	42 hours	90 hours
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
68	4	30	48	22	74	94
523	6	76	78	19	64	88
550	35	89	93	23	85	97
5194	88	98	98	36	88	98
Difference required for significance:						
Odds 19:1		10.65			7.50	
Odds 99:1		13.86			9.88	

The larger difference between varieties 68 and 5194 in rate of germination disappeared when the naked seeds that had been removed from the pericarp were germinated and used as the basis for comparison (table 2). In 19 hours after the naked seeds had been placed on cotton in the Petri dishes, variety 68 had 22 percent germination, while variety 5194 had germinated to the extent of 36 percent. The results of the final counts (192 hours for seed balls as compared with 90 hours for naked seeds) are even more striking. When seed balls were used, there was a difference of 50 percent in germination percentage between varieties 68 and 5194. When naked seeds were used, this difference was reduced to 4 percent. This suggests that the main factors causing large differences between varieties in germination rate are to be found in the pericarp of the seed ball and not in the true seed.

RATE OF WATER IMBIBITION BY SEED BALLS OF THREE VARIETIES

A measure of the rate of water intake by the seed balls of three of the varieties studied affords evidence that the differences in germination are not due to variation in rate of water imbibition. Three 20-gm. lots of air-dry seed balls of varieties 68, 550, and 523 were weighed out, tied in cheesecloth bags, and submerged in distilled water to a depth of 1 inch. At the end of each soaking period a complete set was centrifuged, at a uniform rate of speed, for 2 minutes. The seed balls were then weighed, and the percentage of moisture imbibed was calculated. It will be seen from table 3 that seed balls of the slow-germinating variety 68 imbibed water as rapidly as did the other varieties. It was further observed that there was only a small increase in the rate of germination when the seed caps were pried loose from the seed balls, leaving the naked seed exposed directly to the moisture and air in the germinator but in contact with the pericarp.

TABLE 3.—*Comparison of rate of water imbibition by seed balls of three sugar-beet varieties*

Variety No.	Water intake on air-dry basis after—		
	2 hours	5 hours	22 hours
	Percent	*Percent*	*Percent*
68	83	100	116
550	70	84	113
523	88	94	113
Difference required for significance:			
Odds 19 : 1		7.6	
Odds 99 : 1		10.6	

TOXIC EFFECT OF WATER EXTRACTS FROM SUGAR-BEET SEED BALLS

The existence of water-soluble substances in the pericarp of sugar-beet seed balls, which affect both rate and total germination of the seed, was shown by the following experiment. Water extracts from seed balls of each of the varieties, made as described, were used in the Petri dish germinations with naked seed of variety 68. Germination started very slowly, and after about 60 hours the sprouts turned brown and died. Normal germination and growth took place

in the dishes where water had been used to moisten the substratum. The toxic effects produced by the extracts obtained from seed balls of the four varieties apparently varied inversely with the rate and total seed-ball germination (table 2); that is, the extract from the seed balls of variety 68 was most toxic to the naked seeds in the test, and the extract from 5194 was least toxic. The other two varieties, which are more or less intermediate in rate of germination of seed balls, took that position in the toxicity of their seed-ball extracts.

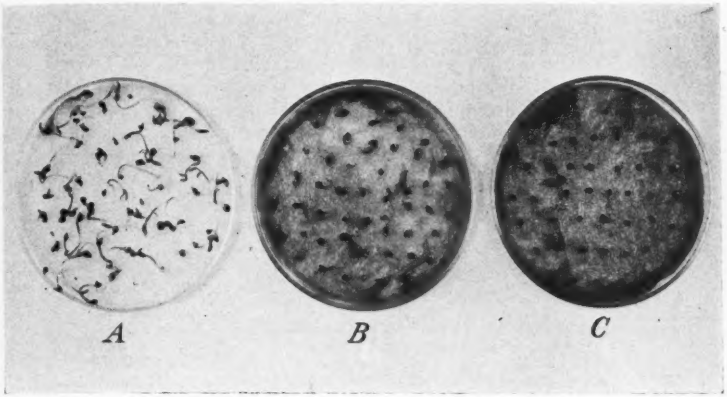

FIGURE 1.—Comparison of the toxic effect of water extracts from seed balls of two varieties of sugar beets: *A*, Check, substratum moistened with water; *B*, substratum moistened with water extract from seed balls of variety 550; *C*, substratum moistened with water extract from seed balls of variety 68. The discoloration of the cotton substratum by the seed-ball extracts is evident. Both inhibition of germination and injury to sprouts that germinated are apparent.

This is partly shown by the data in table 4. The data in the table do not, however, give a complete picture of the injury that occurs.

TABLE 4.—*Effects of water extracts from the seed balls of sugar-beet varieties on germination of naked seeds of variety 68*

Variety from which seed-ball extract was obtained	Germination of naked seeds in contact with seed-ball extracts after—		
	19 hours	42 hours	90 hours
	Percent	*Percent*	*Percent*
68	0	4	7
523	13	35	45
550	16	44	57
5194	22	50	62
Water	60	89	97
Difference required for significance:			
Odds 19 : 1		8.69	
Odds 99 : 1		11.29	

This injury is better shown by figure 1, which illustrates both the inhibition of germination and the injury to the sprouts that did germinate. Almost complete inhibition of germination is shown in figure 1, *C*, where the cotton was moistened with the water extract

from seed of 68. In figure 1, *B*, where the cotton had been moistened with an extract from seed of variety 550, more than 50 percent of the seeds germinated, but the sprouts soon turned brown and died after 60 hours.

CONCENTRATION OF TOXIC SUBSTANCES NOT CONSTANT

The amount of toxic substances present in the sugar-beet seed the varied not only with variety but also within seed lots of the same variety grown in different years or localities, and it is possibly affected by any one or all of the following factors: Climate, soil, and maturity of the seed when harvested. Extracts were made from seed of U. S. 34 that had been grown at different localities in different years. It can be seen from the data in table 5 that the toxicities of the extracts were not constant for the different seed lots of the same variety.

Further tests, involving seed samples of the same variety grown the same year and in the same locality but on widely differing soil types, indicated that soil variation was an important factor influencing the amount of toxic substances in the seed ball.

TABLE 5.—*Variation in the amount of toxic substances present in the seed balls of U. S. 34 grown at different localities and in different years*

Year and locality where seed was grown from which extract was made	Germination of naked seeds after—		
	19 hours	66 hours	114 hours
	Percent	*Percent*	*Percent*
Sandy, Utah, 1932	1	14	32
St. George, Utah, 1933	2	13	31
Granger, Utah, 1934	10	44	61
Hurricane, Utah, 1935	11	51	67
Hemet, Calif., 1935	2	20	45
Logandale, Nev., 1936	0	21	40
Difference required for significance:			
Odds 19 : 1		12.31	
Odds 99 : 1		17.24	

EFFECT OF CONCENTRATION OF THE TOXIC SUBSTANCES

Decrease of rate and total germination was proportional to the concentration of the extract. When any of the extracts were diluted with water the damage to the germinating seed was decreased. The same dilution effect was also apparent when seed balls were thoroughly washed in water before the extract was taken. This reduction in the toxicity of the diluted extracts is shown in figures 2 and 3. The reduction in toxicity is evidenced by an increase in rate and total germination of the naked seed in contact with the diluted extract and also by the more normal development of the sprouts.

The toxic action of seed-ball extracts on germinating seed was not confined to the effect on seed removed from the pericarp, but was also evident when intact seed balls were used. The effect of the toxic substance already present in the seed ball can be accentuated by adding more extract so that the germination rate is further reduced, or its effect may be lessened by washing out some of the toxic substance normally present in the seed ball. In one test, seed balls of variety 550 were soaked for 24 hours in a water extract made by soaking a given weight of seed of 550 for 20 hours in five times its weight of water. The germination of this seed was then compared with that of seed

which had been washed for 24 hours in running water. The results of this test are shown in table 6.

Variety 550, which is a moderate carrier of substances having a toxic effect on germination, was greatly reduced in both rate and total germination when soaked 24 hours in a previously prepared extract from

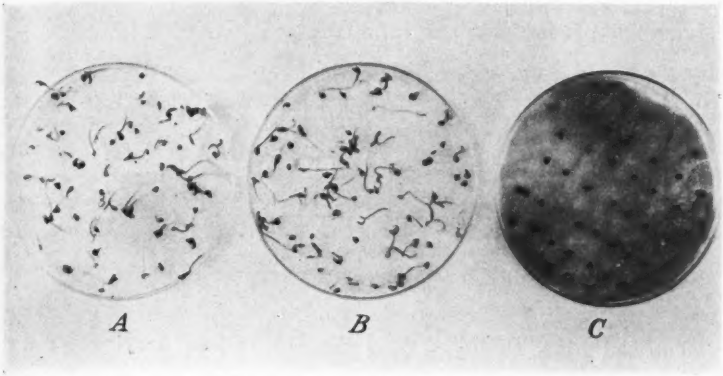

FIGURE 2.—Effect of washing the seed balls prior to obtaining the extract: *A*, Substratum moistened with water: *B*, substratum moistened with a water extract from seed balls of variety 68 that had been soaked and dried prior to making the extract; *C*, substratum moistened with a water extract from seed balls of variety 68.

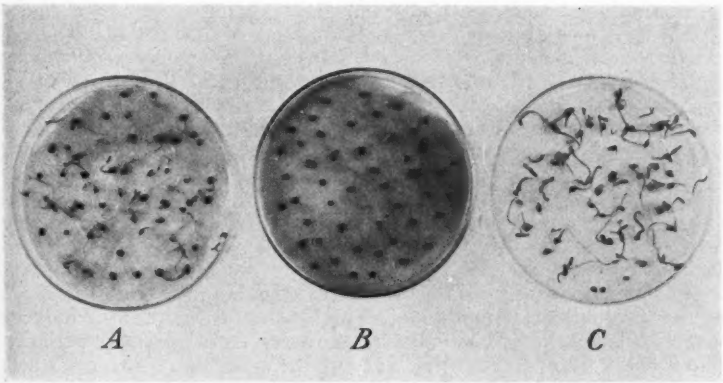

FIGURE 3.—Effect of diluting the extract after extraction from the seed balls: *A*, Substratum moistened with an extract fom seed balls of variety 68 that was diluted 2:1 with water; *B*, substratum moistened with regular extract from seed balls of variety 68; *C*, substratum moistened with water.

the same seed. The reduction in germination of variety 550 soaked in extract was not so great as the reduction in the germination of seed of variety 68, which was alternately soaked and dried three times, the same water being used for each soaking. The injury resulting to variety 68 from such treatment could not be overcome by subsequently washing the seed balls in running water. On the other hand, when seed

balls of variety 68 that had had no previous treatment were washed in running water there was a remarkable increase in both rate and total germination. It is also evident that the amount of benefit to be derived from washing seed is dependent on the amount of toxic substances carried in the seed balls of the variety and that it is unsafe to soak seed balls of a slow-germinating variety, such as 68, in a small volume of water prior to germination. Enough water to insure proper dilution should be used, and running water gives best results.

TABLE 6.—*Comparison of the rate of germination of seed balls of two varieties in which the amount of toxic substance had been modified by soaking or by washing*

Variety and treatment given seed balls	Germination of intact seed balls after—		
	24 hours	90 hours	192 hours
Variety 550:	*Percent*	*Percent*	*Percent*
Soaked 24 hours in extract from seed balls of 550	0	30	46
No treatment	21	43	70
Washed 24 hours in running water	41	54	81
Variety 68:			
Soaked and dried 3 times (same water)	0	2	7
Soaked and dried 3 times (water changed)	7	34	89
Washed 24 hours in running water	16	56	92
No treatment	0	13	44
Difference required for significance:			
Odds 19:1	13.50		
Odds 99:1	17.55		

COMPARISON OF SOAKING AND WASHING AS METHODS OF REMOVING TOXIC SUBSTANCES FROM SEED BALL

Presoaking of sugar-beet seed for 2 hours prior to making germination tests is recommended by the Association of Official Seed Analysts of North America (*19*). It is desirable that this recommendation be expanded to specify an adequate amount of water to insure removal of toxic substances from the seed ball. Experiments showed that variation in the quantity of water in which seed was soaked or failure to wash and properly dry samples after soaking caused variations in the results.

Table 7 gives the data obtained from an experiment to test the effect of presoaking sugar-beet seed in different quantities of water and the further effect of washing or not washing the seed balls after the presoaking period. Seed of two varieties was used, 68 and 550. The seed of 68 is a heavier carrier of the toxic substances; the seed of 550 carries only moderate amounts. The *F* values (*17*) in table 7 indicate that there is a real difference between the behavior of these two varieties. The *F* values show further that varying the quantity of water in which the seeds were soaked had a marked effect on subsequent germination. Washing the samples for 5 minutes in running water after the soaking period also had a marked effect, and it will be further seen that the 5-minute wash period after soaking was of much more importance when small quantities of water were used for presoaking.

Further comparison between the effectiveness of soaking and washing the seed balls for different lengths of time prior to germination is given in table 8. It is evident that washing in running water was more effective than soaking for the removal of toxic substances and that washing up to 6 hours was beneficial. Washing beyond 6 hours was of no apparent advantage.

TABLE 7.—*Comparison of the effect of different quantities of water used to presoak sugar-beet seed, and the further effect of washing the samples in running water for 5 minutes after the 22-hour soaking period*

GERMINATION DATA

Treatment of seed balls prior to placing them in Petri dishes to germinate		Germination of intact seed balls					
		Variety No. 68			Variety No. 550		
Volume of water used to soak seed 22 hours	Treatment following soaking	42 hours	114 hours	218 hours	42 hours	114 hours	218 hours
		Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
3 times weight of seed	Washed 5 minutes	12	48	60	16	44	58
	Not washed	1	20	28	11	36	47
6 times weight of seed	Washed 5 minutes	15	48	61	29	51	69
	Not washed	3	39	54	15	38	46
9 times weight of seed	Washed 5 minutes	14	46	64	33	62	69
	Not washed	9	41	61	27	49	66
16 times weight of seed	Washed 5 minutes	23	54	70	37	66	75
	Not washed	12	51	68	35	55	67
Washed 22 hours in running water.		18	73	80	38	63	76
No treatment given seed.		0	12	45	1	37	63
Difference required for significance:							
Odds 19 : 1		12.0					
Odds 99 : 1		15.6					

COMPARISON OF CALCULATED *F* VALUES WITH *F* VALUES FOR THE 5- AND 1-PERCENT POINTS

Source of variation	Calculated *F* value	Significant *F* values	
		5 percent	1 percent
Between varieties	63.73	3.94	6.90
Washed and not washed	114.69	3.94	6.90
Between quantities of water used for soaking	48.47	2.70	3.98
Washing or not washing × different quantities of water	13.10	2.70	3.98
Variety × washing or not washing × quantity of water	15.10	2.70	3.98

TABLE 8.—*Comparison of the effect of soaking seed in 5 times its weight of water and washing seed in water for varying periods of time*

[Test with variety 68]

GERMINATION DATA

Treatment	Germination of intact seed balls after —		
	4 days	6 days	8 days
	Percent	*Percent*	*Percent*
No treatment	8	29	50
Soaked 3 hours	17	35	65
Washed 3 hours	16	39	78
Soaked 6 hours	23	47	75
Washed 6 hours	41	76	88
Soaked 24 hours	15	41	74
Washed 24 hours	38	79	87
Difference required for significance:			
Odds 19 : 1	11.5		
Odds 99 : 1	14.82		

TABLE 8.—*Comparison of the effect of soaking seed in 5 times its weight of water, and washing seed in water for varying periods of time*—Continued

COMPARISON OF THE CALCULATED *F* VALUES FOR THE 8-DAY COUNT WITH *F* VALUES FOR THE 5- AND 1-PERCENT POINTS

Source of variation	Calculated *F* value	Significant *F* values	
		5 percent	1 percent
Between replications	3.45	5.59	12.25
Between hours of treatment	13.74	4.74	9.55
Between soaking and washing	10.32	5.59	12.25
Soaking or washing × hours of treatment	2.45	4.74	9.55

It seems rather important that where presoaking is made a part of laboratory procedure, it should be done in standard containers of sufficient size to allow for an adequate volume of water; otherwise

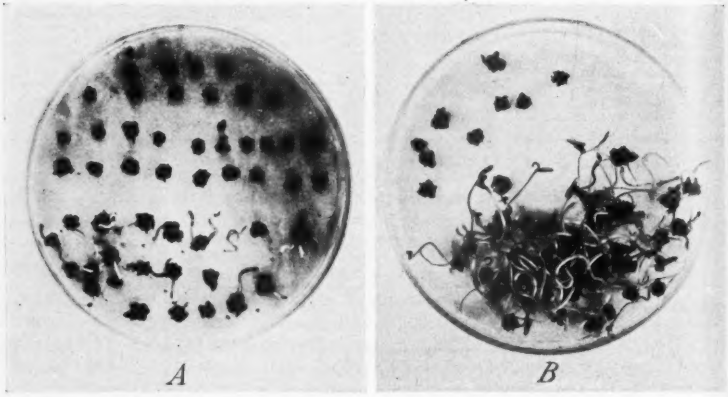

FIGURE 4.—Comparison of the condition of sprouts from seed balls not washed and those washed prior to germination in Petri dishes. *A*, Unwashed seed balls of variety 550, 1 week after they had been placed in a Petri dish on cotton moistened with water. Damage to the sprouts by the substances that arise from the seed ball is very apparent. *B*, Seed balls of variety 550 that were washed 22 hours in running water before being placed on moistened cotton in a Petri dish. The healthy appearance of the sprouts is apparent even after 2 weeks of growth.

the seed should be washed in running water. The appearance of the sprouts in blotter germination tests readily indicates whether the seed balls are being properly presoaked or washed. If the tips of the sprouts become darkened during the test, this is evidence that toxic substances have not been properly removed from the seed balls. Figure 4 shows the condition of sprouts from seed balls that had been thoroughly washed and from seed balls that had not been washed prior to being placed in Petri dishes to germinate. Possibly it should be pointed out here that when sugar-beet seed is germinated on cotton in Petri dishes it is somewhat more sensitive to the presence of toxic substances than when it is germinated on blotting paper. However, practical experience in several seed laboratories has shown this same relationship to apply to blotter tests.

DRYING SEED BALLS AFTER SOAKING OR WASHING

The importance of freeing the seed balls of all excess moisture, after washing or soaking and before placing them in a moist chamber to germinate, was demonstrated on several occasions. Figure 5 shows a comparison between the percentage germination of seed balls placed on moist cotton immediately after washing and the percentage germination of seed balls that were air-dried after the washing process.

It seems advisable that some standard procedure should be adopted that will insure removal of the excess moisture that might interfere with respiratory processes of the germinating seed. Practical experience of several seed laboratories seems to indicate that thorough blotting removes sufficient surface moisture to prevent the difficulties as outlined above.

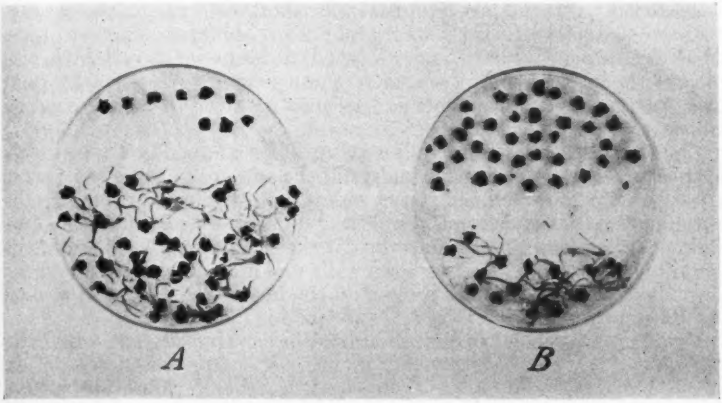

FIGURE 5.—Cultures showing the importance of properly drying the seed balls after the presoaking period and before placing them in a moist chamber to germinate. *A*, Seed balls air-dried after washing, before being placed on cotton. After 5 days, 82 percent showed visible sprouts. *B*, Seed balls placed on cotton immediately after washing. After 15 days only 28 percent had germinated.

DISCUSSION

The finding that water-soluble subtances toxic to germinating seeds exist in the pericarp tissue of sugar-beet seed balls and the demonstration that these can be removed by proper washing afford an explanation for the improved germination that has been found to result from washing or soaking sugar-beet seed. In regard to the so-called "stimulating effects" from liquid seed treatments with inorganic salts or fungicides, the possibility that the effect has been brought about by removal of toxic substances should be taken into consideration. In some experiments by C. H. Smith, of the Salt Lake City laboratory, as well as in the early experiments of Stehlík and Neuwirth (*18*), it was found that water alone was as effective in increasing germination as solutions of various inorganic salts. Hanley and Woodman (*7*) and Garner and Sanders (*6*) report that treatment of sugar-beet seed balls with sulfuric acid leads to an increase in both rate of germination and total germination. They attribute the increase in germination to a greater permeability of the hard seed balls, which allows the processes connected with germination to take place

more rapidly. Stehlík and Neuwirth (*18*) give data to show that this effect is no greater than that obtained by soaking in water. It is obvious that decortication by sulfuric acid removes some of the corky material of the seed ball and with it some of the toxic substances. This treatment is also followed by thorough washing, which, in itself, would remove some of the toxic materials. Inasmuch as both washing in water and soaking in sulfuric acid result in the removal of toxic substances from the seed ball, it is to be expected that both treatments would result in increased germination.

The substances in sugar-beet seed balls that produce the toxic effect on germination are probably accumulated in the pericarp during seed development. It is possible that chemical changes in these substances take place during seed germination; however, since the toxic effect is produced by substances located in the pericarp rather than in the true seed, the primary source of these substances does not appear to be germination byproducts as has been reported in lettuce seed by Shuck (*16*).

The fact that seed from different varieties and different seed lots of the same variety may vary widely in the amount of toxic substances present makes it difficult to give a generalized statement regarding the benefits to be derived from presoaking. The amount of benefit to be derived from presoaking, the length of the presoaking period, and the advantage of washing as compared with soaking will all depend on the amount of toxic substances present in the lot of seed used and also on the substratum on which the tests are made.

Varietal differences in germination due to the presence of toxic substances are most clearly shown on the cotton in Petri dishes. When blotters, sand, or soil are used as the germinating media, there is a gradual decrease in the toxic effect proportional to the ability of the substratum to remove substances from the seed ball. This is similar to the finding of Borriss (*2*), who concluded on the basis of tests with *Vaccaria pyramidata* that the germination-promoting effect of the soil was not due to the presence of any stimulative factor, but rather to the removal of an inhibitory substance from the seeds by the absorptive power of the soil complex. Experiments by the authors indicate that in the field the effect of toxic substances is so reduced that, although the effect on rate of germination may be noticeable, little effect on total germination and no effect on yield have been apparent. Since the purpose of laboratory tests is to forecast the field performance of seed, it is desirable to guard against interference from toxic substances. Inasmuch as they do sometimes interfere in blotter tests, it seems advisable to include their removal in the germination procedure. Proper washing and drying of the seed balls prior to placing them in the blotters will increase the rate of germination, avoid damage to the sprouts, and reduce the variation between samples.

SUMMARY

Seed balls from different varieties of sugar beets varied widely in rate and total germination even though an equivalent number of seed balls from each variety was known to contain mature seed. These differences between varieties were largely dissipated when the naked seeds, removed from the seed ball, were germinated or when seed balls from the different varieties were thoroughly washed prior to the germination test.

The amount of water-soluble substances present in sugar-beet seed balls varied not only with variety but also within seed lots of the same variety grown in different years or localities, and is possibly affected by any one or all of the following factors: Climate, soil, and maturity of the seed when harvested.

Water-soluble substances present in the seed ball were found to produce a toxic effect on germinating sugar-beet seed, both retarding germination and killing the radicles. This effect may be a very important factor among lots of sugar-beet seed in causing the differences observed in rate and total germination of seed lots in seed laboratories.

The adequate removal of these substances from the seed ball seems to be advisable in laboratory procedure where blotters or similar substrata are being used for germination tests. Inasmuch as the amount of toxic substances varies with variety and within different seed lots of the same variety, it seems advisable to recommend a laboratory procedure that will insure their removal from all seed samples.

The water-soluble toxic substances of sugar-beet seed balls can be removed by either soaking or washing in running water, a 6-hour period of treatment being adequate for their removal from seed balls carrying large amounts of the toxic substances. Soaking the seed in a sufficient volume of water to insure dilution of toxic substances was definitely beneficial, but not so effective as washing the seed in running water.

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